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VOL. 84

THE TSETSE FLIES OF EAST AFRICA

A FIRST STUDY OF THEIR ECOLOGY, WITH A VIEW TO THEIR CONTROL

BY
C. F. M. SWYNNERTON
Director, Tsetse Research Department, Tanganyika Territory

With a Preface by
THE RIGHT HON. W. ORMSBY-GORE, M.P.
Secretary of State for the Colonies

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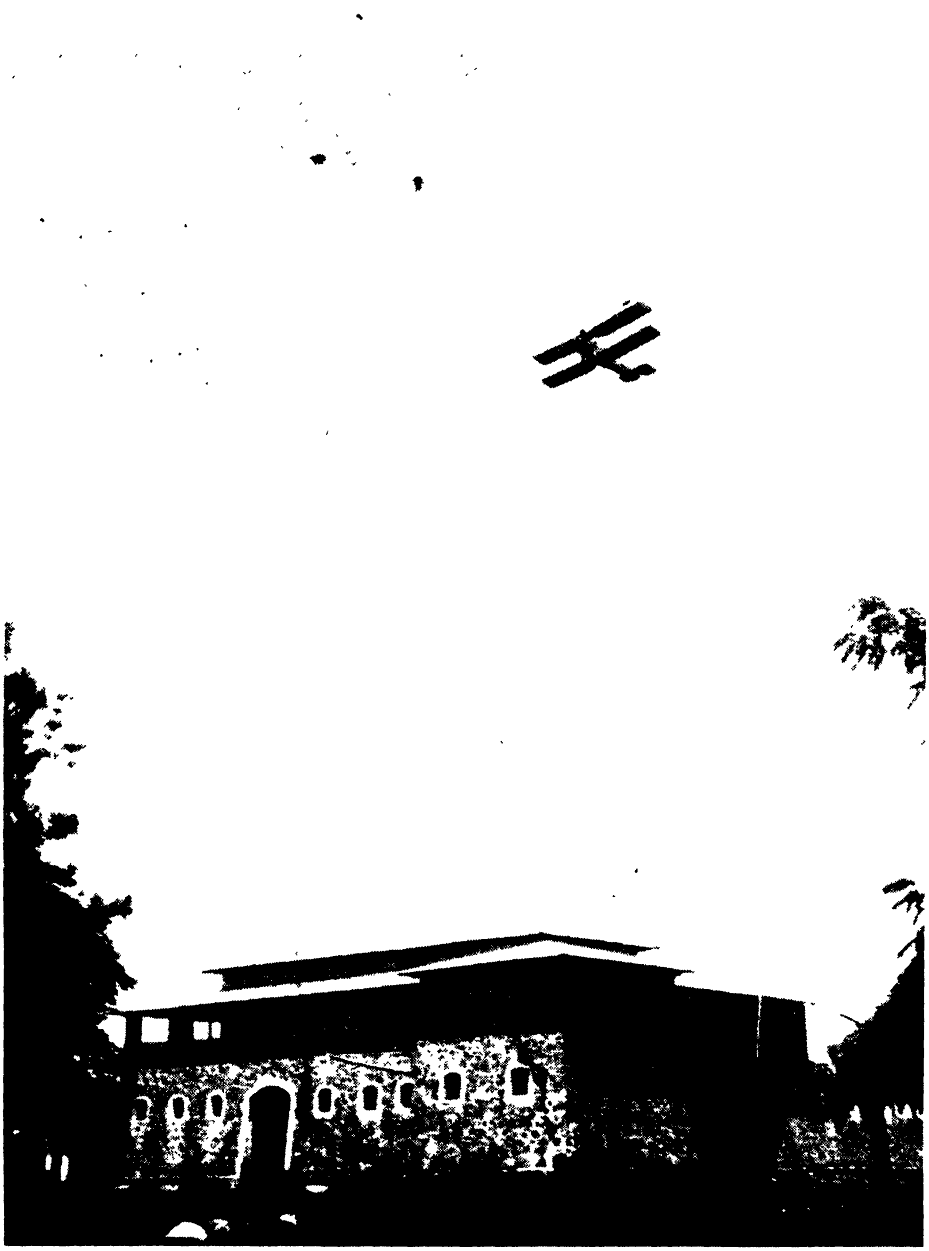

The "Boma," or old German fort, at Old Shinyanga, which contains the offices, laboratory, museum, herbarium, and (above) two of the residential quarters of the Tsetse Research Department, Tanganyika.

Above it is one of the Government aeroplanes which carried out the aerial photographic survey from which many of the illustrations in the present paper have been taken.

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PREFACE

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THE RIGHT HON. W. ORMSBY-GORE, M.P.,
Secretary of State for the Colonies.

In this volume the Director of Tsetse Research in the Tanganyika Territory, Mr. C. F. M. Swynnerton, gives a comprehensive account of the present state of our knowledge in regard to the problem of the tsetse fly in east Africa. As is well known there is scarcely a question of greater importance for the future development and well-being of the British and other territories in that part of the world. The future prosperity of considerable tracts of Africa depends on whether it will be found possible with the aid of science to devise means by which they can be inhabited by man and his domestic animals without risk of infection by human or animal trypanosomiasis. At present these infected areas are sparsely inhabited and their development retarded by the presence of the tsetse fly which acts as the carrier of these diseases. The question whether effective steps can be taken to control the tsetse fly in such a way as to permit of the development of these areas is therefore one of great social and economic importance to the Administration of every one of the Territories affected.

I was much struck during my visit to the British East African territories in 1924 by the urgency as well as by the importance of the problem. To take the case of Tanganyika alone, it is not merely that some two-thirds of the Territory are already under fly, but there is moreover a constant danger of further encroachment. Even within the last few years between two and three thousand square miles have been lost to the Territory by the advance of the fly into areas which might have been expected to be strong enough to withstand its assault by reason of their possessing good grazing, good soil, an ample water supply, and a native population traditionally attached to the country. These losses have been only partly counterbalanced by the excellent work which is being done in reclaiming areas already infested by the fly.

A problem of this magnitude clearly calls for action both by those charged with the responsibilities of administration and by scientific investigators. An important step in this direction was taken in 1925 when the late Lord Balfour appointed a special Tsetse Fly Committee of the Committee of Civil Research (now the Economic Advisory Council) to draw up a programme for a concerted attack on the tsetse problem in the British Territories in east and west Africa. The programme so prepared has formed the basis on which the work of the last eleven years has been developed. Greatly increased funds have been made available, scientific staff has been recruited, and new organisations have been developed for investigating the many and varied aspects of the tsetse problem. At the request of successive Secretaries of State, the Tsetse Fly Committee has continued to act as the adviser of the Colonial Office on questions relating to trypanosomiasis and tsetse fly control, and has formed a valuable link between the workers engaged in research work in Africa and their scientific colleagues both at home and in other parts of the world. At the same time steps have been taken to ensure that administrative officials and research workers

in Africa should have opportunities of discussing with one another the problems in which from their respective points of view they are all so deeply concerned. In recent years these discussions have been placed on a more formal basis by the institution of periodical conferences, at which the various branches of the problem have been passed under review.

The evidence gained from the work of the last few years has shown how complex is the nature of the tsetse problem and how varied are the measures that will be required for its solution. That this should be so is no matter for surprise when it is recalled that in east Africa alone there are eight species of tsetse fly, differing widely from one another in their natural history, in their habits, and in the type of country which they can inhabit, but all alike capable of acting as the carriers of disease.

No man has played so large a part in the attack on the tsetse problem as Mr. Swynnerton, Director of the Tsetse Research Department in Tanganyika. As early as the time of my visit to Shinyanga in 1924, he had begun the experiments in control measures, which, with the increased staff and funds that have since been made available, have done so much to show how the various species of tsetse may be controlled, their advance checked, and territory reclaimed from their grip. No one, therefore, could be better qualified than Mr. Swynnerton to review the present but still limited state of our knowledge of this subject.

In the present work Mr. Swynnerton has brought together both the evidence secured by himself and his collaborators in the course of their work in Tanganyika, and that obtained by workers elsewhere, which has hitherto been available only in scattered publications in scientific literature. Mr. Swynnerton's survey of this subject will be of exceptional interest not only to scientists, but also to all concerned with, or interested in, the development of tropical Africa.

(*Signed*) W. ORMSBY-GORE.

Colonial Office,
October 1*st*, 1936.

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PART 1.—INTRODUCTORY, FINANCIAL, AND ADMINISTRATIVE.

A.—INTRODUCTORY.

The present paper covers in the main the work of the Tsetse Research Department, Tanganyika Territory, from January 1931 to December 1934. It is long, but with so much to report and discuss, it seems best frankly to make it a book on tsetse flies, and to refer those who have not the time to read it to the table of contents for the subjects that interest them and to the comprehensive summary with which it concludes. Just what advance has been made and whether, as well, we are justifying our claim to take from the tsetse the land that it is holding in trust against the time when man shall become wiser in his use of it, may be judged most quickly from the summary.

For greater completeness, a number of observations from outside the period and areas strictly covered by the present paper are included, in particular Dr. G. B. Wallace's unpublished observations on *G. austeni* Newstead and *G. brevipalpis* Newstead; and, to serve as cementing material, old knowledge and observations of my own—seeing that the report is in effect a summing up of our work and our present knowledge. A brief history of the work and a contrasting of old methods with new have been included on account of their general interest.

Further, if the reader should ask why botanical description and discussion figure strongly in a report upon flies, I reply that the view expressed in 1919 (Swynnerton, 1921 : 317) that "the practical study of tsetse is a matter for the botanist and ecologist rather than the unaided entomologist" has been amply borne out by experience.

Unevenness in treatment and detail and any repetition that may be found are apologised for on the score that, though the report took a long time to write, not nearly enough time was available for the purpose. For this reason also, work in territories other than Tanganyika is less fully dealt with than would otherwise have been the case.

Keys to the identification of east African tsetse flies and their pupae are given in appendix 10.

B.—THE PROBLEMS AND THE PRESENT ATTACK.

1.—THE PROBLEMS AWAITING SOLUTION.

(a) The broad position in Africa.

It is well known to-day that by far the greater part of tropical Africa, amounting to some four and a half million square miles, is under infestation by the tsetse, that in the greater parts of the areas under infestation, cattle cannot be kept, and that in a vast proportion of them sleeping sickness still takes its toll of the human population despite the high efficacy of modern drugs and a huge expenditure on staff and organisation, treatment and segregation, in the various countries concerned. If one draws a line from the Senegal river on the west coast through Lakes Chad and Rudolph to a point half-way up Italian Somaliland, and a second line bisecting Angola, dropping south on reaching Northern Rhodesia, then bisecting Southern Rhodesia west to east, it is possible to say that the vast bulk of the country between these two lines, a band nearly 2,000 miles wide, is infested with one or other of the twenty-one species of tsetse fly and is a hot-bed of human or animal trypanosomiasis or both. Outliers occur in Arabia, Abyssinia, the Sudan, and Zululand.

The tsetses, it is true, have in the past performed an invaluable duty in saving great areas of country from becoming peopled, exhausted and ruined,* but now that we are here to regulate settlement and prevent erosion, we wish to see a stop put to the destruction of people, the exclusion of cattle and the obstruction to development; and, if we are prepared to do our duty to the country reclaimed in the way indicated, we are justified in attacking the tsetse. Otherwise we are not.

(b) The extent of the established infestation in east Africa.

(i) *The Tanganyika Territory.*

The extent of the established infestation in Tanganyika may be seen at a glance on referring to map 1. Reference is made on pp. 54–56 to that of the different species. The solution of the problem is of as great importance to Tanganyika as to any country in Africa; for, of this Territory, measuring 366,000 square miles, about two-thirds are already infested and in the remaining third infestation has been going forward with startling rapidity.

Eight species of tsetse are concerned in the infestation of Tanganyika, namely, *Glossina morsitans* Westw., *G. swynnertoni* Austen, *G. pallidipes* Austen, *G. austeni* Newstead, *G. palpalis* Rob.-Desv. var. *fuscipes* Newstead and var. *martinii* Zumpt, *G. brevipalpis* Newstead, *G. fuscipleuris* Austen, and *G. longipennis* Corti.

(ii) *Kenya.*

The most recent Kenya fly map, compiled by Mr. C. B. Symes, Medical Entomologist, and including amongst much else the results of recent safaris by the Veterinary Entomologist, Mr. E. A. Lewis, shows :—

(i) A coastal belt of tsetse 180 miles broad, extending northward to Ras Miamboni, and inland, (*a*) on the railway, to Makindu with occurrences beyond, (*b*) to a greater distance up the Tana, (*c*) as scattered records in the country between that appear indicative of a fairly generalised infestation. The flies are *G. brevipalpis*, *G. pallidipes* and *G. austeni* on the coast, *G. pallidipes*, *G. brevipalpis* and *G. longipennis* between the railway and the Tanganyika border, and *G. longipennis*, *G. pallidipes* and flies unidentified between.

(ii) Small belts of *G. pallidipes* south-west of Fort Hall, south-west of Laikipia, north-west of Natron, and in the Lambwe Valley in South Kavirondo.

(iii) A belt of *G. pallidipes* and *G. longipennis* that extends from north of Mount Kenya to Marsabit and, with breaks, west to the Uganda border.

(iv) An important belt, continuous with fly belts in Tanganyika, on the Amala (Mara) river and east and west of it; *G. swynnertoni*, *G. fuscipleuris* and *G. pallidipes*, in addition to much *G. palpalis* var. *fuscipes* on the Kavirondo lake-shores and rivers.

(iii) *Uganda.*

In Uganda (as maps received from the Chief Entomologist show) tsetses of one species or other occur across the north of the country from West Nile through Nimule and Kitgum well into Karamoja (*G. morsitans* and, chiefly, *G. palpalis*); down the Albert Nile and Lake Albert to Fort Portal (*G. morsitans*, *G. palpalis*, and *G. pallidipes*); then southwards to Lakes Edward and George inclusive (*G. palpalis*, *G. pallidipes*, *G. morsitans*, *G. fusca* (Walk.)); between Mbarara and the Tanganyika border (*G. morsitans*), from south of Lake Salis-

* See p. 464 below.

bury (north-west of Mount Elgon) to Tororo (*G. palpalis*); and a belt of *G. pallidipes* east of Jinja. *G. brevipalpis* and *G. fuscipleuris* also occur.

The main problem in this country of lakes, swamps and rivers, is, naturally, *G. palpalis*, but a fair proportion of the country is affected by one tsetse or another.

(iv) *Northern Rhodesia.*

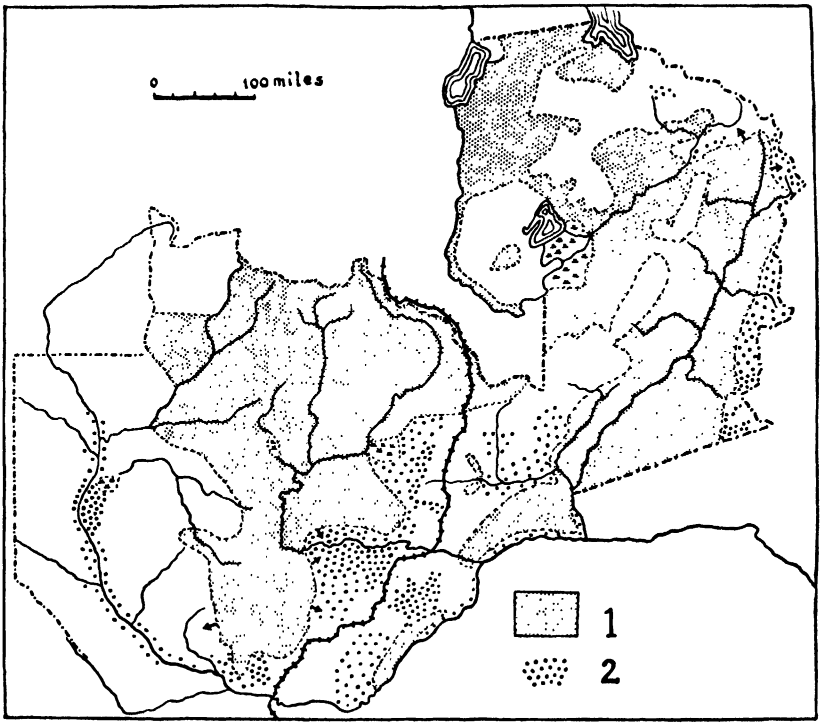


Fig. 1.—Map of the tsetse-fly areas of Northern Rhodesia, mainly of *G. morsitans*, from Prof. Alan Ogilvie, 1934. The bounding line on the south is the Zambesi river, and there enters it, flowing eastward (midway along), the Kafue, and, flowing south-westward (on the right), the Luangwa. The lakes are Mweru on the north-west, Tanganyika (south end) to its right with the Abercorn *morsitans* belt below it, and, further south, Lake Bangweolo, with the Chambezi flowing into it.

Professor Alan Ogilvie's map of Northern Rhodesia provides data regarding the infestation in Northern Rhodesia. The Colony is extensively beset with *G. morsitans*; and *G. palpalis* occurs on Lake Tanganyika. A broad strip on either side of the Zambezi and of the railway as far north, about, as Kashitu, is uninfested and, in large part, carries cattle. The whole great central block in between is infested with *G. morsitans*. In the north-eastern portion of Northern Rhodesia, the Luangwa valley from north to south is the centre of a very broad belt of *G. morsitans*. Another belt of considerable extent fills the country south-east of Lake Mweru, from the northern border of the colony round to the western. Between the two and connected with each lies a third belt, bisected by the Chambezi. Taking all these belts into account, it would seem that the country is infested in nearly as high a proportion as is Tanganyika.

(v) *Nyasaland.*

Nyasaland has been heavily invaded of late years by *G. morsitans* and *G. brevipalpis* also occurs there. A map kindly supplied by Dr. W. A. Lamborn * shows small belts of the former fly in, or partially in, every one of the twenty district except six—Ncheu, Central Shire, Chiradzulu, Mlanje, Cholo and Lower Shire. The most heavily infested districts are those of Kasungu, Fort Manning and Dowa flooded by the invasion referred to above that has been held up in the borders of Lilongwe. Upper Shire has considerable infestations as well. There is a more scattered infestation in South Nyasa, while a band of fly stretches across the north of Mombera and a much broken band lies between hills and lake in Kota-Kota, Dowa and Dedza.

(vi) *Summary.*

Summarising as regards established infestation, it is safe to say that fully half the area of these five territories combined is infested with tsetse fly and under the very severe handicap to settlement and development which this entails.

Extensive areas also are affected with human trypanosomiasis, Rhodesian sleeping sickness carried by *G. morsitans* and *G. swynnertoni*, and Gambian sleeping sickness carried by *G. palpalis*, the last only in limited lake-shore and riverine strips. Biharamulo, the whole Western Province, Musoma, Mkalama, Manyoni, Utete and Kilwa are amongst the districts in Tanganyika in which outbreaks or cases due to *Trypanosoma rhodesiense* have occurred—and been taken vigorously in hand. The distribution of the tsetse *G. palpalis* in east Africa, given broadly on p. 159, is, or not long ago was, nearly coterminous with the range of *T. gambiense*.

(c) Advances by the flies into new country.

The uninfested area amounting to about one-third of the whole of Tanganyika has been diminishing with startling rapidity. Owing to the fact that the inhabitants of the areas invaded are cattle-keepers, such areas are actually lost to development, since, except for rare villages that cling despite all, the people retreat in front of the fly when their stock begin to die, and great stretches of country revert to wilderness. In addition, much of the country still uninvaded is ruined by over-stocking and consequent erosion. To quote the very interesting annual report for 1931 of the Director of Veterinary Services, " it is not as though loss of available pasture and an appreciable mortality were the beginning and end of the trouble; before fly-enroachment cattle owners flee and crowd their animals into areas already overstocked; thus every year the tendency is towards greater concentration of stock in smaller and smaller areas. The resultant overstocking has already given rise to a serious problem of erosion. . . ."

In Nyasaland a similarly rapid advance took place during recent years. In Southern Rhodesia a great area in the north of the country, infested before the great rinderpest outbreak of the nineties, has since been steadily re-infested. In the north-eastern portion of Northern Rhodesia, the notorious Luangwa belt is extending in a most dangerous manner.

Advances by fly into new country in Tanganyika were already taking place strongly and unresisted when the territory was in German occupation.

* Reproduced here as fig. 2.

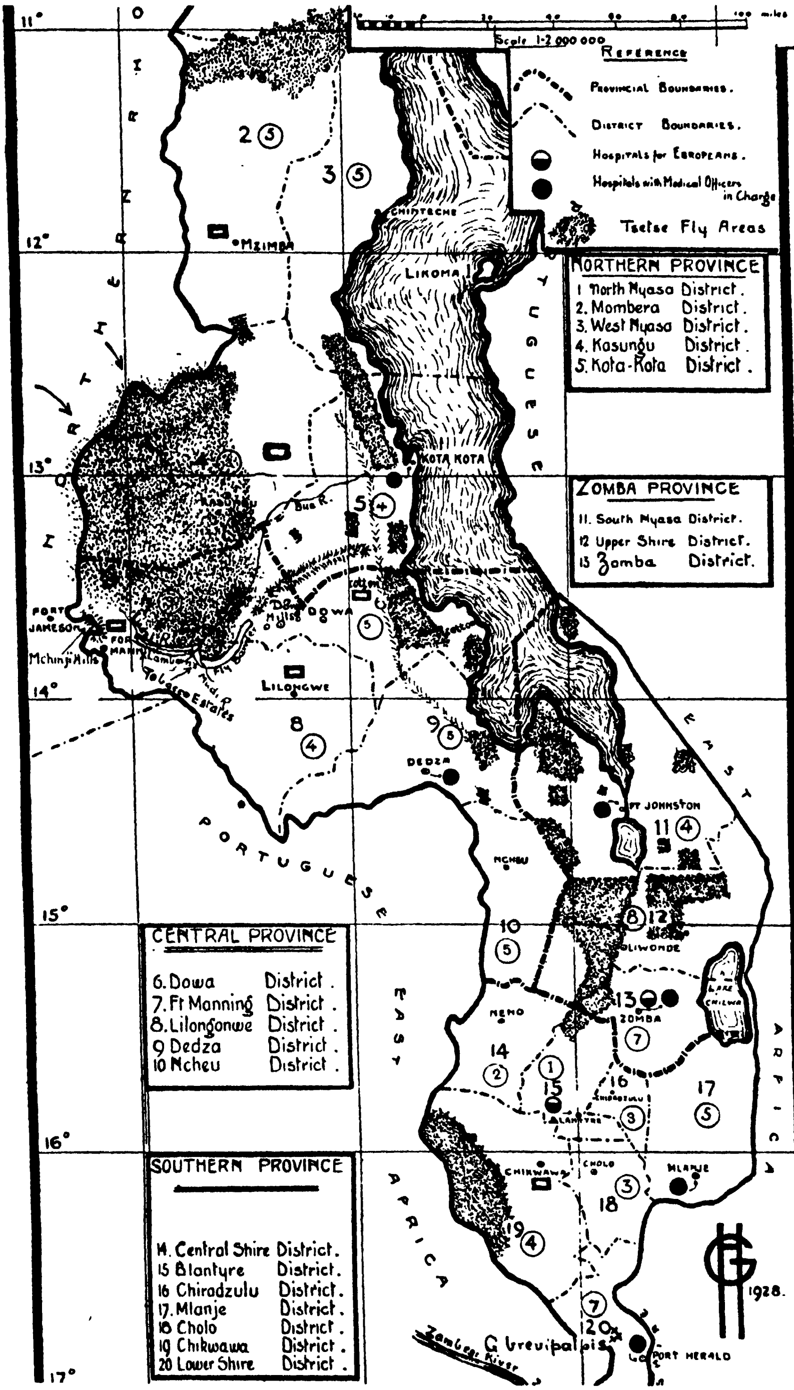


FIG. 2.—Map of the tsetse-fly areas of Nyasaland (*G. morsitans*). Lamborn's barrier is shown in the centre. Monkey Bay is north-west of Fort Johnston.

That the tsetse problem—or problems—even of east Africa alone—are of a most menacing nature and of the first economic importance may be sufficiently gauged from the outline given in this and the preceding sub-section.

(d) The nature of the problem.

There are eight species of tsetse in Tanganyika, seven in Kenya, seven in Uganda, and of each it can be said that owing to its different requirements, predilections, and habits, it constitutes a problem of its own. This is not all. The tsetses are bound up with their vegetational habitats, and each of the several types of country in which a species of tsetse occurs presents at least a different sub-problem. It is like the song of the little nigger-boys: as one type of country is provided for by our measures, others remain. Having at this moment perhaps three measures in view for this most widespread of the tsetses, we are still left to find rhymes for seven types of country which *G. morsitans* afflicts. The *G. morsitans* of western Singida, the *G. morsitans* of Handeni, the *G. morsitans* of the Ugala river, the *G. morsitans* of Nigeria—and so on—each requires differing treatment. This, and the fact that there are twenty-one species of tsetse in all, each species with its sub-problems, and the fact that, owing to the vast areas concerned, the measures for each sub-problem must be cheap, will give some idea of the magnitude and complexity of the problems that a tsetse investigation has to solve. In these two respects—diversity and extent—combined, no other entomological problem approaches it. And it brings in, for necessary study, an astounding variety of subjects: the fly itself—each species separately—its distribution, habits, movements, senses, requirements—which differ with the season—reactions and economic status; protozoological problems; man, his habits in relation to the flies and theirs in relation to him; the domestic animals in their relation to the fly and to trypanosomiasis; nearly the whole vertebrate population except fishes, as food or as enemies—each species separately, for each has a different contact or a different food value with the tsetses, and a different one for each species of tsetse; the various vegetational types, each being friendly or inimical to one or the other of the numerous species of tsetse or to one or the other of its activities; geology and elevation as helping to determine the vegetation, and the soil in relation to the latter and to the pupae of the flies; meteorological phenomena generally in their effect on the harbouring vegetation and soil, and, also, directly, on the tsetses; the study of eco-climates and ecidio-climates—those, that is, of the vegetation types and of places that the tsetses hide in; administration—for breaking the contact of the natives with the infection, for their proper settlement or re-settlement, and the awakening of their interest and action in contribution to the solution of their problem; medicine, human and veterinary, for curing or protecting them and their cattle; agriculture and development generally—as one means of expelling the flies and of consolidating gains; engineering—for the possibilities of flooding them out or producing mechanical devices for trapping them, or—through "tanks," rollers, pneumatic secateurs and saws, and Boadicea scythes—destroying their homes; the parasites and fungoid diseases of the flies; chemistry—lethal gases, tree and insect poisons, repellent and attractive substances, including the gland extracts of mammals; methods of clearing the various vegetational types; experiments in modifying these—by partial clearing, grass-fire organisation or grass-fire prevention—just to the point at which the change in eco-climate resulting will be inimical to the tsetse concerned; forestry—for the reconciliation of the need for clearing with that of the preservation of gum-arabic and useful timbers and for the pro-

duction of unfriendly vegetational types as barriers to fly advances; barriers and fences generally, against the flies and their food animals; the reconciliation of such game control as the tsetse research organisation may need to put into effect with the (important) requirements of game preservation; the means of providing water in the lands reclaimed for settlement; and last, but not least, soil erosion—as may be seen on p. 400 below. Laboratory work and large-scale experimental attack in the field, applied measures, constant co-operation with half a dozen government departments and the handling of great bodies of labour all come into the picture, as does the aeroplane—very vitally—to produce adequate preparatory surveys.

It is an amazing problem, it demands a variety of staff, much of it needs long-range work. No one who had any glimmering of the nature of the problem should have expected spectacular results in the period of a very few years that the present investigation has been in progress.

2.—THE HISTORY OF THE TANGANYIKA TERRITORY'S ATTACK ON THE TSETSE PROBLEM.

(a) Survey (1921–22), and experimental and tribal reclamation (1923–1927).

I was Game Warden but had had experience of tsetse work, when in 1921 I was entrusted with a survey of tsetse distribution in the Tanganyika Territory. This was done and a tsetse map made, and, in view of previous observations and of observations then made, preliminary experiments were carried out at Kilosa in methods of clearing and to determine the effect of late grass-burning on *G. morsitans*.

In 1922, I decided that if support were forthcoming, I would attempt a large-scale experimental attack on a tsetse situation with a view to applying such knowledge and ideas as were already available, to gaining further experience and especially to learning what practical difficulties faced us and should be investigated. It was hoped that a special team for research and reclamation combined might be provided later. I was begged by the Senior Commissioner, Tabora, Mr. H. C. Stiebel, to locate this attack in Shinyanga in view of the seriousness of the situation in that area.

The Colonial Office at this stage invited proposals and the scheme just referred to was sanctioned.

Detailed exploratory surveys were carried out and Shinyanga was actually chosen as the site of operations. It was decided to attempt at the outset to ascertain (i) whether an annual voluntary out-turn of a native population could be organised to attack their own problems; (ii) whether natives could be persuaded to settle in places in which their presence would consolidate gains made or assist in making them; and (iii) whether by postponing and organising the annual grass-fires tsetses could be driven from good grass country.

In West Shinyanga, a great retreat had for some years been taking place in front of an advance by the tsetse, *G. swynnertoni*. Thirty thousand people had already evacuated the chiefdom concerned—" Shinyanga "—which had given its name to the district. Between three thousand and four thousand persons remained and these were leaving rapidly. Mr. C. McMahon was District Officer at the time and meetings were held at which we exhorted the people to stand fast and to combine in a scheme of attack against the fly which the government would help them to organise.

The chiefs and people responded splendidly and, after a small preliminary beginning in November 1923, ten thousand men came out from the chiefdoms

generally and worked for a month in 1924 under the guidance and supervision of Mr. S. P. Teare (Game Ranger), myself, and our game-scouts. They placed a cleared barrier in front of the fly advance which, with settlement behind it and organised grass-fires within it, it has never since passed; they made a great 24 square mile clearing in the piece of country (Kizumbi) that still retained some little settlement, with a view to turning the tide (fig. 3); they made a beginning with a scheme of splitting up the fly belt into blocks in which different measures could be tried out and the clearings between which would hinder the return of the flies into any block from which they might have been driven; and some of the contingents did work as well in their own special sections of the district.

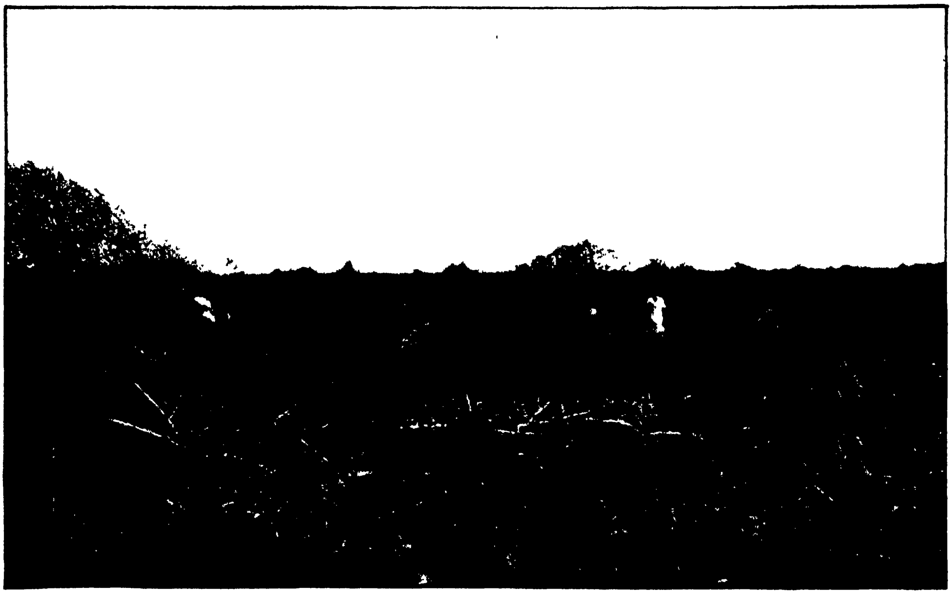


FIG. 3.—Kizumbi Bay, close to Chief Wamba's village, when cleared in 1924. Flies (*G. swynnertoni*) were then still present in the felled wooding. Lying trees *Acacia spirocarpa*. The authorities for the plant names used in the present paper are given in appendix 7.

Settlers began to enter the district in 1923 and this influx gradually overtook and outstripped emigration. Inducements were given including an acre plot annually in a large cotton field, which, after having personally trained the oxen and drivers, we ploughed, and which has since been transferred from the Tsetse Research Department to the Department of Agriculture and is to-day the important Lubaga Agricultural Station. Many of the younger new settlers were taught later by Mr. Teare to plough and took to it keenly (fig. 4). The first instalment of the controlled grass-burning campaign took place in 1924, and, in a country then swarming with tsetse, produced spectacular effects.

In the years immediately succeeding, most of the work was performed by the chiefs and their people in their own chiefdoms, but such labour as could be spared for the main campaign pushed slowly on with the splitting of Shinyanga into " blocks " (see map 2), while additions to the work in Nzega produced an extensive safe area between the Manonga river and the station of Nzega

itself. Other districts also called on our Department for help. In 1925, Mr. B. D. Burtt and Mr. F. A. Montague, who had just joined the Department as Reclamation Officers, supervised clearings in Mkalama which held up fly advances and Mr. Burtt did similarly useful work for the Wambulu. Mr. H. S. Magnay replaced Mr. Teare on leave in 1925, and between the latter, Mr. Magnay and Mr. Montague, work was begun in Maswa. In this area the need for additional supervision became apparent, the natives, though willing, being less crusade-like in spirit than had been those in Shinyanga. The present rule that there should be one European to supervise each five hundred men was then first laid down.

The year 1922 saw the discovery in Mwanza of the first-known outbreak of Rhodesian sleeping sickness outside Rhodesia and Nyasaland and the

FIG. 4.—The first field ploughed at Lubaga, Shinyanga, in 1924–25. S. P. Teare teaching incoming native settlers to plough. Chiefs on right.

inauguration by Dr. G. Maclean of sleeping sickness measures, which have since been developed by him on a large scale. In this year *G. swynnertoni*, which had previously been collected by the Germans and by Mr. W. F. Fiske, was first distinguished from *G. morsitans*.

The year 1925 may prove to have been a red-letter year, for it was in it that Swedi bin Abdallah, head fly boy, showed, and Mr. W. H. Potts, Mr. B. D. Burtt and Dr. Wallace confirmed, that continuous low thicket in adequate width * is not favoured by *G. morsitans*. It was known already that where fires are excluded from savanna wooding " for several years . . . the result, when this occurs so far from high (rain) forest as not to obtain seeds from it, is a form of dense thicket " (Swynnerton 1917 : 508). The two observations together suggested possibilities of control.

* Pl. 17.

(b) The great advances by the flies in the Central Province during the years 1926 and 1927.

In 1926, it was realised that great invasions of country by tsetses were taking place (i) in the Masai steppe near the borders of Kondoa-Irangi (*G. swynnertoni*), (ii) from north-western Kondoa into Usandawe and westwards towards Singida * (*G. morsitans*), and (iii) (also *G. morsitans*) eastwards from the Tabora boundary into western Singida.† The Tsetse Research Department was specially asked to attend to these areas. Mr. Potts and Mr. Burtt were, therefore, employed on a thorough survey of them. As a result of this survey it was definitely concluded that if these areas were not dealt with vigorously they would inevitably submerge all western Kondoa and all but the open country of Singida. As the task was obviously going to be one of importance, extending over several years and involving much work and expenditure, and as research on *G. morsitans* was also projected, it was decided to open a station at the most central site, Kondoa-Irangi. At the same time, work was begun against the advances by fly into Usandawe and western Singida.

(c) Tsetse research alone (1928–1930 inclusive).

Late in 1924 the members of the East African Commission had visited the tsetse work in Shinyanga, and after walking over the ground, were impressed with the scheme and its initial promise. Largely through the keen interest in the problem shown by Major Rt. Hon. W. G. A. Ormsby-Gore, then Parliamentary Under-Secretary of State for the Colonies, what is now the Tsetse Fly Committee of the Economic Advisory Council was established in London in the following year by the late Earl of Balfour, then Lord President of the Council, and Chairman of the Committee of Civil Research, of which at first the present Tsetse Fly Committee was a sub-committee. On its recommendations " a scheme of organisation that affected all the Crown Colonies in Africa was drawn up. Under it two main investigatory organisations were recognised : one in Nigeria under Dr. W. B. Johnson and Dr. Ll. Lloyd, one in Tanganyika under Mr. C. F. M. Swynnerton" (*Trop. Agric.*, **10**: 237). I had urged (1921 : 317) *that only by investigation on ecological lines, never applied to them previously, were these problems likely to be solved*, and I had asked for a team of entomologists, a zoologist, botanists (the latter to include above all a trained ecologist) and field officers to carry out the practical measures in the field. I went to America specially to seek an ecologist, but finally found and selected Dr. J. F. V. Phillips, then Forest Research Officer in Knysna.‡ The team ultimately materialised as such late in 1927, when intensive research was begun.§ Early in 1929 the Tsetse Division of the Game Department became a separate Department, with headquarters at Kondoa-Irangi. Reclamation, however, and participation in the work against the great fly advances of this area, ceased to be our concern, and three Reclamation Officers were transferred from the Tsetse Research Department to the administration.

For the Department a period of pure research followed, during which, however, I personally re-started experimental reclamation in Shinyanga in

* Map 5. † Map 6.

‡ The "ecology" of an animal or plant, or animal and plant community, is simply its "natural history," but the use of the term implies that the latter is being studied on certain organised lines on the basis of the plant or animal's relation to its surroundings or "home" (Greek, Οἶκος, home, Λόγος, study), whether the environmental influences are being exercised by climate, geology and soil, vegetation or animals.

§ For the list of staff, see p. 17 below.

August 1929 on a limited appropriation which I received for the purpose. I had always been convinced that the only way to tackle this great field problem was by a combination of research and large-scale reclamation scientifically watched. The former would show what the flies required and suggest means of depriving them of their requirements, while the latter would test the ideas gained and bring to light the difficulties, which research could then set out to solve. Unfortunately, when sufficient staff was available for experimental reclamation, the research team had not been formed, and, when the latter materialised, there were no longer facilities for reclamation available. The special *raison d'être* of our headquarters at Kondoa had disappeared also, and we later returned to Shinyanga.

(d) Research and reclamation in combination (1931–1934 inclusive).

The special spell of research was of value, for there was leeway to make up, and the partnership between the two sides that was first planned in 1923 was at long last brought about in December 1930 on the urgent recommendation of the Tsetse Fly Committee of the Economic Advisory Council. The usefulness of the combination may be judged from the account of the work done by the team during the past four years that is contained in the present report. Large-scale field experiment has been the order of the day for the executive staff, as, also, has been work on behalf of the administration and tribes which has brought us into touch with variations of the problem and with all kinds of practical difficulties in a really invaluable manner. The research staff has worked on the bionomics of the fly, has investigated situations in the field, and has attended to difficulties.

The return of our headquarters to Shinyanga has given a new lease of life to our original scheme of reclamation—experimental and tribal, combined in a productive co-operative effort. After the great initial attack on the western Shinyanga problem in 1923–24 it was ruled that each chief's annual contingent should so far as possible work only in that chief's area. The campaign for the expulsion of the fly came to depend on some small contribution in labour each year for a scheme which had been intended (i) to provide methods for the use of *all* chiefdoms, and (ii) by providing large new areas for grazing to relieve the heavy over-grazing and erosion taking place *in the whole* settled area. The tribal effort became dissipated annually in a series of small and widely separated local clearings, some of them of little real use, many of them poorly executed. The central scheme thus became rather disorganised. The arrival of our headquarters and an adequate staff in Shinyanga, the energetic prosecution of anti-tsetse measures by ourselves with some money to spend on it, the backing of a keen administration and the revival of interest which was added to by our being able to hand back to this section of the tribe in 1932, Chibe, its traditional birthplace, which had been lost to the flies many years earlier, gave new impetus and quality to the work. Further, a middle path seemed suggested whereby, while retaining popularity for the work by catering for local wishes, such parts of the central scheme as would specially interest a chiefdom were allotted to it to carry out. But whereas in the beginning all the work was experimental, including the employment of the tribe, to-day no tribal labour is employed on experimental work.

Larger contingents have in this way been available and have been employed as described. Thus the Mwadui and Usiha contingents were used on the cattle corridor (see map 2) which gives them access to the great north-western plains, and Lohumbo, Usule, and Usanda are contributing labour to the

similar break-through from their side on the left of the map. In addition, being now in a position to survey and supervise for them, we are helping the outlying chiefdoms of Shinyanga with such schemes of their own as we regard as being of value. The clearings connected with these schemes we are so guiding that instead of the wasteful, marginal "trench-warfare" clearing that was the vogue in all work but our own, these chiefdoms are cutting off large blocks of bush country for us to attack by our methods (map 3).

All such work has been the direct result of requests through the administration from the various chiefs that we should direct work in their chiefdoms. Both the chiefs and their people seem generally grateful for our help and pleased with the results obtained.

In addition, since 1933, we have, by invitation, extended our activities almost to their former range, by including within them surveys and guidance of clearings and clearing campaigns in Nzega, Maswa, Kwimba, Musoma, and Mwanza (Msalala)—map 3—and Kahama, Mbulu and Pangani.

Further, we have been called in to advise on problems in Kenya and Uganda. Close co-operation has been built up between ourselves and the workers in these two territories. Workers yet further afield (*e.g.* in Fernando Po and the Anglo-Egyptian Sudan) have also been assisted with information.

3.—METHODS, PIONEERING AND MODERN.

It is interesting to contrast the organisation and methods imposed on us in the pioneering days of the work with those of to-day. The tsetse staff at the start was made up of the half-time services of two individuals, the remainder of their time being devoted to "game." The means of transport used were foot and bicycle. Occasionally a Ford car was hired by the senior of the two, a scout was taken, two bicycles were lashed outside the car, and on reaching the path that led ultimately to the survey or the clearing to be marked out, visited or supervised, there would be tied to the bicycles tea-making material, a saucepan, a blanket, a mosquito net, and the scout's mat and blanket. The officer would remain out for one or more days, living on food bought from the natives until he returned to the car. Our assistants on the clearings were game-scouts converted into labour supervisors, but, when instructed, wonderfully efficient. With them, and by dint of hard riding and hard propaganda, lavish encouragement and explanation of the objects in view, and through the chiefs, who came out in person and encouraged similarly with the metaphors of battle—as well as through the very whole-hearted backing of the Senior Commissioner and District Officers—we ran with success a reclamation campaign in two districts with the help of many thousands of natives, the results of which stand good to-day. Fire-control over an area of 1,700 square miles, fly-pickets, large catching-out experiments, a ploughing station, surveys and assistance to settlement were carried on also: work never ceased till dark. Later, when Mr. Teare was alone, the extinction of grass-fires at night, night lions, and night garden-raiders engaged his additional attention. None of us in those days knew a great deal about office work except our excellent Indian clerk, A. V. Thakur, far away in Kilosa; and when mails overtook me, I used to work nightly till twelve or two in the morning to overtake correspondence, there being no time for this in the day. These were shocking secretarial arrangements and earned much disapproval, but in the circumstances they provided the only way of getting the campaign really going.

The addition of expert staff, each man with his specialised share of the work, and the specialised development of the office organisation by Mr. N. H.

Vicars-Harris, at first a Reclamation Officer, later Secretary, and now Assistant Director, have changed the scene greatly. No longer is there such anxiety as to the over-expending of votes, and clerical work—typing of reports, accounting, costing, correspondence, etc.—is taken off the hands of the officers in the field by the office. The value to the officers in the field of the time so saved and of the interruptions so averted has been very clearly shown in their output. When all allowance has been made for the small size of the Tsetse Research Department in Tanganyika, it would be difficult to find a department better organised and with a better run office than ours is to-day, or one with a general organisation better suited for its purpose.

So far as Shinyanga is concerned, roads, made or temporary, radiate from our centre to every large piece of work that we are doing; three departmental lorries carry labour, water, stores and safaris here and in other districts; and every officer has his car. In these circumstances work and further organisation become, admittedly, easier, but the energy put into the former is unreduced, the keenness and output are great and any risk that there might be of the personnel becoming softened is still averted by the hardships of wet-season surveys, night work (for one or two) on the burning of fire-breaks, and, generally, by work in the bush.

4.—THE BROAD POLICY OF TSETSE CONTROL IN THE FUTURE.

As regards the broad policy of tsetse control to be adopted in the future, probably three schools of thought may be found:—

(i) Those who favour retreat—in other words evacuation of the fly country generally in favour of concentrated settlements which will keep the bush and, therefore, the tsetse down in the area of settlement, followed by slow expansion of that area, such expansion being assisted by organisation of agriculture. This method, with or without this assistance, has necessarily been put into effect in most sleeping sickness countries as a result of the need for removing the people as quickly as possible from intimate contact with infection.

(ii) Those few who still asseverate that only by a holocaust of the game animals can the tsetse be destroyed.

(iii) Those, like ourselves, who, in the course of our work, have become optimistic regarding our power to expel the flies from large areas of bush without destroying the wooding, and who advocate a nice balance between accessibility of native settlement to the public services and utilisation by it of wider areas of country. Those of this school of thought believe also that discriminative game expulsion will be a part, here and there, of the measures to be adopted, but that no general extermination will be necessary.

Each of the above views will be considered in turn. To these have been added a sub-section (sub-section (*d*)) on tribal clearings, and a brief note (sub-section (*e*)) on immunisation.

(a) Reliance on the complete clearance of bush which will result from the presence of concentrated and expanding settlement.

The concentration of settlement produces very great advantages in the form of accessibility to administration, medical treatment, education, agricultural improvement, and transportation facilities. We should see, doubtless, that population close up to fly bush would hold its ground and that, with its own increase and that of its agriculture, organised by us, it would advance

gradually against the fly bush. On the other hand, while such a policy might get rid of the tsetse in the course of the next few hundred years, when the entire country had become thickly settled, it would involve the complete destruction of the natural forests which, we, in our investigations, are trying to spare; it would never give the populations concerned the elbow-room which they require for really rapid expansion, such as (financially) would be invaluable to this and most African territories in a period when it is most needed; and, however well it was organised, it would, by itself, tend to produce a growing enlargement of the overstocked, eroded areas, comparable in nature with cancers, that to-day are a subject of so much anxiety.

Secondly, such a policy would abandon to the invading flies by far the greater part of the remaining uninfested portions of the country. Thirdly, the adoption of general retreat followed by this form of trench warfare would mean that we have despaired of controlling the tsetse—a despair to which we refuse to subscribe.

(b) Game destruction.

The killing of game by natives will *not* produce much relief. Unchecked hunting by natives has gone on intensively in numerous areas during my long residence in Tanganyika Territory and in Portuguese East Africa, but the natives neglect areas where they have made the game scarce (yet still ample to feed tsetse) and hunt it where it abounds. The only certain effect ever noted has been the *spread* of the tsetse thereby by the movements of man and game which this form of hunting engenders. Further, it was this type of hunting which some years ago was leading to the diversion of the natives from the planting of crops and which by one Provincial Commissioner at least was discouraged for this very reason. It is exactly this kind of hunting that has constantly given rise to highly infected foci of sleeping sickness at tsetse-infested hunting camps in the bush that bounds the settlements of natives.

Highly organised hunting by paid European staff with paid native assistants is different, and in certain open types of wooding will result in success; but it entails great expense over a period of years, is liable to be an indefinite commitment and in fairly dense cover is incapable, as our observations seem to show, of success. This is fully discussed on pp. 225–228 below.

(c) The policy recommended.

Effective direct or indirect attack on the fly in the bush is obviously the only full solution, as and when we become able to prescribe measures for one sub-problem after another.

A few of the tsetse-fly areas are small in extent and, with the necessary money, could be attacked undivided. Others are very great—*e.g.*, 500 miles by 300 miles. As regards measures that can at present be visualised, *other than advancement of the vegetational succession by not burning the grass*, large areas of this kind must, in most of this country, be sub-divided before they can be attacked.

The preparatory policy, then, for those that need sub-division, would entail:—

(i) after a close vegetational, agricultural, and tsetse survey, the selection of lines for isolating barriers to enclose great blocks of tsetse-infested bush, and would consist of (*a*) naturally open or cheaply openable spaces, (*b*) bush-types, sufficiently wide, unsuited to the tsetse concerned, (*c*), for *G. morsitans* or *G. swynnertoni*, continuous wide thicket, or country that by not burning

the grass would go to such thicket, and (*d*) clearings, tribal or other, and settlement;

(ii) the steady formation of the barriers as opportunity offers;

(iii) the destruction of the tsetse in the blocks of bush that have been isolated by the barriers.

Where natives are available, the barrier settlements would be formed partly by the judiciously sited concentration of scattered villages. It has long been suggested that these settlements, and any formed in connection with sleeping sickness concentrations, should be so placed that while they take advantage of water, present or provisible, and selected conditions of soil, they also fall within the proposed barrier lines. Their agriculture would be so organised as to secure the gradual extension of these lines, till they coalesced with other settlements or with thicket or open-ground sections, thus ultimately completing the barriers. "The enclosed blocks would then be attacked by whatever measures are found, on investigation, to fit the area" (Swynnerton, May 1935, *United Empire* **16** : 275–284).

Settlements thus created on picked lines in the bush, like those favoured by the first of the three schools of thought (no. (i) on p. 13 above), at once gain the great advantages enumerated in the address to the Colonial Institute here referred to, but the outlet for the fuller development which would be supplied by the great block that they would isolate is an essential part of the full solution :—

(i) Without it the settlements, like those existent already, will be cramped and become sites for erosion.

(ii) Country free from the fly is a thousand times more attractive to enterprise, native and European, than land under infestation. This, as regards the former, is well seen in Shinyanga to-day, and infested country almost everywhere lacks population because most of the people have left it, or would refuse to enter it, not on account of fear for themselves but because cattle cannot be kept there.

(iii) It is a biological rule that a species of animal, given new country in which the conditions favour it, including an absence of enemies, will increase in numbers more rapidly than in crowded conditions. Man may be no exception, and it is certain at least that the provision of abundant fly-free space and opportunity for extended enterprise into all the picked spots of the country will bring about an increase of prosperity, thereby health, and thereby population and enterprise, wealth and revenue, that are some of our aims in Africa.

(iv) The question of milk comes in also : the natives themselves, where they are cattle-keepers wholly or partly, regard milk as a need of their children.

In general, the expulsion of the tsetse is the key to the economic future of the country, for the fly amongst other things precludes the keeping of cattle, which, besides being a form of wealth in themselves and an anchor to keep people on the land, are an important adjunct to the production of a prolific and healthy native population which in turn is the basis of increased production. On the other hand, the inability to keep cattle keeps natives off the land. The difficulty that we have no large market to-day for our surplus stock does not alter the facts referred to, nor mean that, with further striving (see p. 402 below), we may not yet overtake or regulate increase of stock. Meantime it

may be pointed out strongly that the existing cattle have barely begun to be utilised as an organised source of the manure which the settled land so badly requires for its conservation and development.

A policy of attack is indicated—not one of retreat alone—and to discover how to carry it out and then to guide its conduct is the *raison d'être* of the Tsetse Research Department.

(d) Tribal clearings.

Tribal clearings, initiated with the co-operation of the administration, are invaluable, but where they are made only marginally (as they have often been where we have not guided them), they tend merely to increase the treeless areas that will become overstocked and eroded. Used in this way they provide no good solution.

It is true that the progressively advancing line or ring of tribal clearing, at a safe distance behind which we might allow the bush to regenerate and cattle to graze, which was suggested long ago by myself (Swynnerton, 1924), can be useful if it has behind it the weight of labour and the unbroken annual repetition required to push it on really rapidly. But the upgrowth of uninhabited bush behind is incompatible with permanent agriculture. This method will, therefore, be possible in a few places only. Even where it can be used it will lose most of its usefulness if it is discontinued at the nearest intersultanate boundary.

Employed, however, as in Shinyanga, and now, under our guidance, elsewhere,* as barriers to cut off blocks of bush country for treatment, tribal clearings are an invaluable part of the real solution of the problem, as outlined above, where willing and sufficient native effort is available.

(e) Immunisation of stock.

Immunisation of stock is sometimes urged as an alternative to the destruction of tsetse. Immunisation against protozoal diseases has not met with much success in the past and even if it were to do so in this case (as Bevan's work shows that it may) it is generally agreed that, while extremely beneficial, it would not constitute a complete solution of the problem.

5.—PRINCIPLES GOVERNING ATTACK.

It has already been stressed that the problem is highly multiple and very complicated. The details of the infestation even of a single species of tsetse vary from place to place, and it is also probable that one measure will seldom suffice even for one locality. In most cases a combination of measures will be needed. There will be a main measure, but here local drainage, there some planting, there again settlements sited in a fly focus, and in another case game control, may have to be added.

The combination of measures will vary with the local circumstances, which will have to be separately and expertly appraised. The most useful types of main measure, as I urged many years ago in view of the enormous areas infested and the consequent expense in attacking them, are likely to fall into two categories—(*a*) attack, direct or indirect, on the concentration points of the flies, and (*b*) the utilisation at the lowest possible cost of great agencies already existing. Such agencies were visualised as large native tribes, attacking their problems for themselves under guidance, annual grass fires, flooding (in the

* See map 3 and Block 9 shown on map 2.

very few places in which this may be possible) and the advancement of the vegetational succession by not burning the grass. We have used the first two of these measures with much local success and the last shows great promise. The highly discriminate application of any of these to some one vegetational community, or part of it, that is vital to the tsetse we are dealing with, in its concentration sites only, would combine (*a*) and (*b*) and be obviously an object to be aimed at. That such may sometimes be within the bounds of possibility may be judged from the facts narrated on pp. 56 and 57 below, under "concurrence of requirement" and in Part 3, Section B, under the sub-sections (3, 4 and 10) dealing with discriminative methods (pp. 262–272 and p. 278 below).

An account of our trials of measures, which might be applied to the attack on the great blocks of country that it is proposed that the barriers should isolate, is given in Part 3 of the present paper.

C.—SUPPORT, EXPENDITURE, AND FINANCE.

In Tanganyika we work under the aegis of the Tsetse Fly Committee of the Economic Advisory Council, in London, as do the other tsetse investigators of the Crown Colonies. Our expenditure at present is limited to £15,000 a year, and of this sum £750 is provided by Tanganyika Territory and £14,250 by the Colonial Development Fund. The Territory has, in earlier years, financed the work so generously out of loan funds that, taking its sleeping sickness organisation also into account, it can probably be said that no Territory, British or foreign, has spent nearly so much on the problem as has the Tanganyika Territory since it came under British administration.

D.—STAFF, ORGANISATION, STATIONS, AND THE WORK OF INDIVIDUAL MEMBERS OF THE TSETSE RESEARCH DEPARTMENT, TANGANYIKA TERRITORY.

1.—THE STAFF IN 1930 AND 1934 RESPECTIVELY.

TABLE 1.

The staff of the Tsetse Research Department, Tanganyika Territory, in 1930 and 1934.

Year.	Director.	Deputy Director and Ecologist.	Assistant Director.	Secretary and Librarian.
1930.	C. F. M. Swynnerton.	J. F. V. Phillips.	—	N. H. Vicars-Harris.
1934.	C. F. M. Swynnerton.	—	N. H. Vicars-Harris.	—

Year.	3 Entomologists and Zoologist.	Botanists.	Senior Field Officer.	Observers and Field Officers.
1930.	W. H. Potts. C. H. N. Jackson. T. A. M. Nash. H. M. Lloyd.	B. D. Burtt. G. W. St. Clair-Thompson. J. D. Scott.	—	S. Napier-Bax. V. A. C. Findlay. G. T. Wheeler. J. Y. Moggridge.
1934.	W. H. Potts. C. H. N. Jackson. H. M. Lloyd. J. Y. Moggridge.	B. D. Burtt.	S. Napier-Bax.	V. A. C. Findlay. G. T. Wheeler.

TABLE 1.—*continued.*

Year.	Reclamation Assistants.	Mechanical Assistant.	Asiatic Clerks.	Total.
1930.	C. A. H. Heard. G. Rosch. H. J. Klopper.	—	G. B. Panvalkar. M. C. Desai. D. M. Phatak. R. A. Jamenis.	21.
1934.	H. Harrison. A. Lombard.	G. Rosch.	G. B. Panvalkar. R. A. Jamenis.	15.

2.—THE STATIONS WORKED AND THEIR STAFF.*

(a) Old Shinyanga, the present headquarters.

(i) *Situation, history, and object.*

Kizumbi, three miles south-west of the present New Shinyanga township, was the original headquarters of the tsetse work. As stated more fully already, the latter was shifted to Kondoa-Irangi in 1927 in order better to deal with the great fly advances taking place to the west and east of that area. We moved back to Shinyanga in 1931, on account of the fuller support and better facilities for large-scale work which we had found that we could count on there.

The former German fort at Old Shinyanga, which had formed the British Administrative Station until the latter was moved to New Shinyanga, is our centre to-day.†

(ii) *Staff.*

The headquarters staff consists of the Director; the Assistant Director, Mr. Vicars-Harris; the Senior Entomologist, Mr. Potts; the Senior Field Experiment Officer, Mr. Napier-Bax; Messrs. Harrison and Lombard (Reclamation Assistants); and Mr. Rosch (Mechanical Assistant). The Botanist (Mr. Burtt), stationed in Shinyanga on his return from leave in November of 1934, continued to work mainly outside. Mr. Lloyd (Junior Entomologist) is replacing the Senior Entomologist while on leave.

Commander Blunt has been employed during 1934 in Shinyanga as described on p. 25. At various times Messrs. R. T. Vane, F. J. Gabbutt, H. J. P. Nelson, D. H. R. Lyon, C. Kostelezky, A. C. Robbie and G. Ireland have been temporarily employed also in Shinyanga on the supervision of dry-season clearings and of dams and on the marking out of the plots for incoming native settlement. Mr. Vane and Commander Blunt have been transferred to tsetse work in Kenya Colony.

Mr. G. W. St. Clair-Thompson (Forest Botanist), in Shinyanga when the annual report for 1930 was written, left us under retrenchment in 1932 and is now an Assistant Conservator of Forests on the Gold Coast.

The headquarters staff does not work in Shinyanga solely. Its members visit localities all over the Territory for which advice is required and its field staff supervises operations in other districts as well.

(b) Kikore Ecological Station.

History and objects. The intensive ecological investigation described in previous reports as the object of the Kikore Ecological Station was for practical

* Kizumbi is shown on map 2; the other stations, except Kilifi, are shown on map 1.

† See frontispiece.

purposes closed in June of 1931. Dr. J. F. V. Phillips (Ecologist and Deputy Director) and Mr. J. D. Scott (Research Botanist) then left the Department, the former for the Professorship of Botany at the Witwatersrand University, the latter (ultimately) for the post of Ecologist in the Department of Agriculture of South Africa. Mr. C. A. H. Heard left also for South Africa in November, 1931.

The ecological plots, burned and unburned, have been kept up, but the meteorological readings in them were discontinued in 1931.

(c) Kikore Entomological Station.

(i) *Situation, history, and object.*

Like the Ecological Station a mile away, the Kikore Entomological Station is on the "instep" of the steep eastern Kondoa escarpment and looks across the thorn-bush-covered plains of South Masailand to Kilimanjaro in the distance. It was selected, on Dr. Nash's representation, for its strong infestation with *G. morsitans* and especially for the great variety of its plant communities, clearly demarcated from each other, which made it a fruitful site for close and comparative study. Further, it was situated in a fly belt which, though long, was a few miles wide only, and which in my view promised to be an ideal area for scientifically planned attack after it had been thus thoroughly studied. This hope now seems likely to be disappointed on account of a plan for its complete clearing by the tribe.

(ii) *Staff.*

Dr. T. A. M. Nash (Entomologist), with Capt. V. A. C. Findlay assisting him, was left alone in Kikore from June 1931 till December 1932. He was subsequently appointed Medical Entomologist for Nigeria and has not been replaced. His work in Kikore was taken over by Mr. H. M. Lloyd, Junior Entomologist, in November 1932. It was concluded at the end of February 1933 and the station was closed.

Kikore was re-opened in August 1934 under Capt. Findlay as a headquarters for survey and reclamation work on our part in the Northern, Tanga, and Central Provinces. The initial work embarked on is described on p. 399.

(d) Itundwe.

(i) *Situation, history, and object.*

The station at Itundwe was placed under the same scarp as that at Kikore but 30 miles south of it, with the object of conducting experiments in a *G. morsitans* area on the effect on the wooding and its regeneration produced by burning the grass and by leaving it unburned, by ring-barking, and by felling, etc. Experimental planting of trees and shrubs was carried out also by Mr. St. Clair-Thompson with a view to discovering the best species for use at a later stage in densification measures. Mr. Napier-Bax carried out our first tree-poisoning experiments in Itundwe.

(ii) *Staff.*

The charge of the trees and shrubs and of the burning and non-burning has, since Messrs. Thompson and Napier-Bax moved to Shinyanga, been in the hands of a native caretaker, Mohamedi Oto, who has performed his responsible task exceedingly well.

(e) Kazikazi.

(i) *Situation, history, and object.*

Kazikazi, which is a closed railway station, lies in close proximity to the mighty thickets of Itigi,* which we found formed a barrier to *G. morsitans.* Our object was to find comparatively narrow thicket-necks for experiments on the width of thicket which the flies could cross unaided. Mr. Burtt, reconnoitring from the air, found suitable sites beside Kazikazi and in addition discovered a racquet-shaped area of miombo wooding, very nearly an island and called by us "the racquet," enclosed in the big thicket of Beruda. Examined on foot, this proved to be a diminutive *morsitans* fly belt and ideal for certain experiments. Kazikazi was adopted as a post.

(ii) *Staff.*

Mr. Burtt, with Mr. Harrison (Reclamation Assistant, in place of Mr. C. A. H. Heard) was installed in charge of the work in July 1931. The thicket investigation was completed in December 1933, when the station was closed. It will be reopened for the experiments in the Racquet, should staff at any time be available.

(iii) *Acknowledgments.*

The station house was kindly lent us by the railways, and we are indebted to Mr. C. Gillman, Chief Engineer, for much other assistance as well.

(f) Masiliwa.

Our previous station in this, the West Kondoa fly belt, had been at Sambala, but the fly advance had now long passed that place and I was anxious that Dr. Jackson should keep in touch with it, (*a*) to study its details, and (*b*) in case the Territory should decide on resistance. Masiliwa, a native village on the Kondoa–Singida road, was chosen as being at the head of the advance and a camp costing £15 was erected there in 1931.

Ideal situations, in which the fly advance had to pass between thicket areas, occurred for an experimental attack on a narrowed front that might for ever have taught us how cheaply to meet an advance by *G. morsitans* and also have saved Usandawe; but factors, one of them that of finance in these hard times, prevented resistance from being made and stopped this vital experiment from being undertaken. Dr. Jackson was therefore withdrawn in September 1932.

(g) Musoma.

(i) *Situation and object.*

Musoma was selected as a station owing to its proximity to the island of Riamugasire. It had been found that the parasite *Syntomosphyrum* failed to make good on *G. morsitans* at Kikore owing to an insufficiency of humus in the soil. Riamugasire had very deep humus, in which *G. palpalis* was breeding, and it was selected therefore for a final trial of this parasite. We also wished to carry out a study of the habits of *G. palpalis* on the lines of our studies of *G. morsitans.*

(ii) *Staff.*

Mr. Lloyd was transferred from Kikore with his stock of parasites in March 1933 to Musoma. On going on leave in August 1933, he was replaced in

* Map 1.

Musoma by Dr. Jackson, who in turn gave place to Mr. Moggridge in April 1934. Mr. Moggridge left in June when Mr. Lloyd returned to Musoma from leave. The station was closed, probably temporarily, at the end of November 1934 when Mr. Lloyd had to come to Shinyanga as Mr. Potts was going on leave. The work done is described for the most part under *G. palpalis* (pp. 125–160 below).

(h) Simiyu River (Maswa).

(i) *Situation and object.*

The Simiyu River (Maswa) station was opened in May 1934 owing to our inauguration there of a large experiment in keeping the grass unburned in types of *G. swynnertoni* country which differ from those of Shinyanga. Another reason for opening this station was that we are now planning, guiding, and supervising so much tribal reclamation in Maswa and (nearby) in Kwimba that locally-stationed staff seemed demanded.

(ii) *Staff.*

Mr. Wheeler has been appointed to this station.

(i) Kilifi.

(i) *Situation and object.*

It is considered likely that some of the measures that we are evolving against *G. morsitans* and *G. swynnertoni* will not apply to *G. pallidipes*. It was decided to study this important fly thoroughly, and the only place in which, after search, we have so far found it sufficiently abundant and conveniently placed for the purpose has been Kilifi, on the coast north of Mombasa in Kenya. *G. brevipalpis* and *G. austeni* are present in numbers as well, half a dozen vegetational types are available and the game situation is of interest. The work was opened temporarily in November 1934, and it was continued, with the Kenya Government's permission, when Mr. Moggridge returned from leave late in 1935.

(ii) *Staff.*

Mr. Moggridge, Assistant Entomologist.

(j) Kakoma.

(i) *Situation and object.*

We have done more research work on *G. morsitans* than on any other fly, as befits its importance both in this Territory and in Africa generally. But we have not had the funds with which to carry out experimental attacks on it on the lines which we think likely to be successful, as, through the accident of the prior demand of Shinyanga and the special facilities there, we have done on *G. swynnertoni*. It is most important that the funds should be forthcoming and that areas should at once be selected in which to carry out the proposed field investigation and the large-scale experiments in control. The areas have been selected and Kakoma, a long-deserted bush-village site 60 miles south of Tabora, has been chosen as the site for the station.

(ii) *Staff.*

Dr. Jackson. It is hoped that it may be possible later to station executive staff here.

(k) Maboko Island.

(i) *Situation and object.*

The Maboko Island station, 15 miles east of Kisumu in the Kavirondo Gulf, Kenya Colony, was opened as a joint experiment between the Medical Entomologist, Kenya Colony, and ourselves, to ascertain whether *G. palpalis* could be trapped out in an island of this type; and, if not, what measures would succeed.

(ii) *Staff.*

Milambo Kazila, one of our Chief Native Assistants with one of our fly boys and a Kenya fly boy assisting him was appointed to this station. The work, described in Part 8, Section B (pp. 440–443 below), is proceeding.

(l) Summary of position regarding present stations.

Shinyanga, Kakoma, Kikore, Maswa and Kilifi are now our main stations, each being in charge of Europeans. Mr. St. Clair-Thompson's experiments at Itundwe are being guarded and an important experiment is being carried out on Maboko Island, each under a reliable native assistant.

3.—THE WORK OF THE STAFF IN THE PERIOD UNDER REVIEW.

(a) Administrative staff.

Since Mr. St. Clair-Thompson, Forest Botanist, left the Department, I have added the planting work to my directive and other activities. The latter, as well as my work at Shinyanga, have included safaris of inspection, investigation and advice within the Territory and outside it, and visits to Zululand, Southern Rhodesia, Kenya (three times) and Uganda (twice). A considerable personal investigation of the possibilities of trapping the various species of tsetse fell into the period here covered.

Mr. N. H. Vicars-Harris, Assistant Director, acted as Director from April to June 1931 and May to November 1933, and Mr. W. H. Potts, Senior Entomologist, from March to May 1933, while I was on leave. In addition to conducting the office work (in which he was efficiently replaced while on leave by Mr. Moggridge), Mr. Vicars-Harris has had charge of the actual station in Shinyanga, including buildings and the making and upkeep of roads and aerodromes. He has carried out tsetse surveys in Maswa and Uduhe and formulated schemes of reclamation for those areas. Since the end of October 1934 he has also taken over completely the numerous fly rounds at Shinyanga. He has been enabled to do this by the pitch of proficiency to which he has brought our two Indian clerks, Messrs. G. B. Panvalkar and R. A. Jamenis—both of whom it is desired to compliment on their very fine work—and, by doing it, he has freed the Entomologist, Shinyanga, for fuller attention to his laboratory and other experiments. Previously Mr. Vicars-Harris had replaced Mr. Napier-Bax in charge of the Field executive section when Mr. Napier-Bax was on leave.

As already explained, the office organisation is so arranged as to take all clerical work—accounting, correspondence, costing, etc.—off the hands of the officers in the field, and this arrangement has proved of great value.

(b) Research staff.

Dr. J. F. V. Phillips was Deputy Director and Ecologist during the first six months of the four years under special review. Mr. J. D. Scott was Research Botanist. In this period both these officers were occupied in winding up the

special ecological investigation at Kikore. Dr. Phillips made important contributions to the work and organisation of the Department during his service and, as was hoped, has left its members duly ecologically minded. Both he and Mr. Scott left behind them a reputation for exceptional energy and ability.

When Mr. W. H. Potts, Senior Entomologist, came from Kikore to Shinyanga in June 1932, he had charge of the fly rounds and reconnaissances at that place and of the laboratory work. The latter has included a series of experiments in the reaction of *G. morsitans* and *G. swynnertoni* to various combinations of temperature and humidity, the study (with Dr. Jackson) of the function of the fat-bodies, and a beginning of our proposed work on the preferences of the flies. These experiments are being continued.

Dr. C. H. N. Jackson, "Survey," now "Second" Entomologist, completed his study of the feeding habits of *G. morsitans* at Sambala, watched and studied the fly advances in Usandawe in Western Kondoa, made a study of the hunger of *G. morsitans* and *G. swynnertoni*, its causes, symptoms and effects, developed the technique of computing the fly population in a given area, worked on the relations of fly and game and on fly movements, took his turn on the investigation of the habits and ecology of *G. palpalis*, investigated the fly advances in Singida in preparation for the action described on p. 433 below, and carried out the necessary surveys and investigations for the choice of areas for our future experimental attacks on *G. morsitans*.

Prior to leaving us, Dr. T. A. M. Nash carried out large releases of the parasite *Syntomosphyrum glossinae*, developed a log-trap for pupae, and completed his four and a half year's study of the relations of *G. morsitans* to weather, season, different vegetative types and game movements.

Mr. H. M. Lloyd, Third Entomologist, worked on *G. swynnertoni* at Shinyanga and carried out an attack on a block of country by means of bait-screens used at the feeding-grounds only. Subsequently he handled the parasite work and the study of the bionomics of *G. palpalis*. During his leave he worked under Prof. P. A. Buxton of the London School of Hygiene and Tropical Medicine. He has since acted for the Senior Entomologist (on leave) and has added to the subjects under study the question of the causation of the reduction in numbers of tsetse when grass burning is excluded.

Mr. J. Y. Moggridge, Assistant Entomologist, has been engaged on entomological work almost ever since he came to the Department in 1930 as an "Observer." He acted as assistant to the Senior Entomologist in Kikore till September 1931, when he was transferred to Shinyanga and took charge of the trapping experiments under myself. Since then, after a spell of survey for, and supervision of, reclamation, and some months in charge of our first experiment in the introduction of cattle to the Huruhuru mbugas (p. 389 below), he has (*a*) conducted a series of experiments in the crossing of open spaces by fly, which have yielded important results; (*b*) taken temporary charge of our parasite and *palpalis* station in Musoma; and (*c*) carried out a series of explorative surveys in connection with *G. pallidipes* in Kahama, Nindo, Moshi, Tanga, and south-eastern Kenya. He has shown such success in entomological work that he has now been placed in definite charge of our work on *G. pallidipes* and has been stationed, as stated, at Kilifi. He is to carry out a month's investigation of this fly in Italian Somaliland on his way home on leave.*

* This investigation was duly carried out, with the very fine support of the Government of Italian Somaliland, which it is desired warmly to acknowledge, in February 1935, during the writing of the present report.

Mr. B. D. Burtt, Botanist to the Department but with strong entomological interests, was for two years in charge of our investigation of the capacity of dense, continuous thicket to impede the passage of *G. morsitans*. He also carried out a special investigation in Mpwapwa of the invasion of that area by *G. pallidipes*, investigated the Singida–Usandawe position from the air on several flights and drew from the air a sketch-map of the vegetation of the Singida and North Manyoni districts,* investigated on foot the Hika fly belt and advance, carried out an investigation in North Handeni on which successful measures were founded, and has since been engaged on detailed vegetation surveys of blocks of country under attack by us in Shinyanga. Incidentally he trained the European officers who are under the Sleeping Sickness Officer to some knowledge of plants, and added greatly to our herbarium collection and the number of the Territory's identified plants.

Mr. G. W. St. Clair-Thompson, Forest Botanist, continued in charge of the experimental thicket plantings in Shinyanga up to December 1932, when he left us under retrenchment. He also left behind him a reputation for great enthusiasm and energy.

Mr. H. Harrison, though nominally an Assistant Reclamation Officer, has been engaged entirely on field research. In charge of our Matelele station in the years prior to the period here concerned, he proved himself an observer and careful recorder and was made assistant to the Botanist for the important observations and experiments that were carried out in the Kazikazi neighbourhood from June 1931 to November 1933. Being thoroughly *au fait* with the fly work, having an excellent knowledge of trees, and being a game man first of all, he was, on leaving Kazikazi, placed in charge of our big game experiments, at present in the stage of preliminary observation, which are described on pp. 283–291 below.

(c) Field executive staff.

Mr. S. Napier-Bax, Senior Field Experiment Officer and in charge of the Field Division of the Department, has continued, and largely completed since he came to Shinyanga from Itundwe, a large-scale series of experiments in different methods of clearing applied to different types of trees, including different methods of poisoning them. He has also been in complete charge of all " reclamation," whether experimental or in assistance of tribes, with Captain Findlay, and Mr. Wheeler, Field Officers, Mr. Lombard (permanent Field Assistant) and a number of temporary supervisors engaged each dry season, working under him. With exceptional organising ability he has brought this work up to a very high pitch of efficiency. He has also carried out much survey.

The forte of Captain V. A. C. Findlay, Field Officer, has been survey, of which he has done much of value. He was assistant to the Entomologist (Dr. Nash) in Kikore from December 1928 till August 1932, when he was transferred to Shinyanga. He carried out some excellent supervision of tribal contingents here and in neighbouring districts. With the reopening of Kikore in August 1934, he was placed in charge of it. He has since carried out several surveys, supervised the continuation of large-scale reclamation in Ufiome–Kikore, reopened some of the entomological work in Kikore and taken charge of a new experiment in vegetation densification as a control measure.

Mr. G. T. Wheeler, Field Officer, stationed in Old Shinyanga from January 1929 till May 1934, was in charge of large clearing operations both there and

* Map 6.

in Maswa and Kwimba, under Mr. Napier-Bax, and carried them out with success. He has constituted a liaison officer with the natives through his keen interest in them and their customs and through his popularity with those of Shinyanga.

Mr. A. Lombard has been highly successful in charge of the fire-control operations under Mr. Napier-Bax each year for three years past, and at other times has taken charge of large labour gangs engaged on dam making and clearing. The energetic assistance given to him by Mrs. Lombard in the night burning of fire-breaks is warmly acknowledged.

The temporarily employed European supervisors who have done very satisfactory work on our dry-season clearings have been listed on p. 18 above.

Of these, Mr. R. T. Vane, after some special training, was transferred to the charge of the large-scale attack on *G. palpalis* which the Medical Department, Nairobi, is carrying out with funds from the Colonial Development Fund, which is described on pp. 443–445 below, and in which he is winning laurels.

Commander D. E. Blunt, previously of the Game Department, worked for the Department in a temporary capacity from April 1934 to the end of that year, and became proficient in the subject. He carried out some useful game surveys, made a collection of the glands of game animals, ranging from rhinoceros to impala, for the extraction of scent for experimental use in our traps, and, in particular, carried out some ingenious and successful experiments in the production of continuously and progressively moving tsetse traps, which are described on pp. 249–251 below. He is now carrying out a full investigation of *G. pallidipes* in the Lambwe Valley, South Kavirondo, under the Veterinary Entomologist, Kenya.

Mr. G. Rosch, the Mechanical Assistant, than whom no one works harder, has filled a niche all his own for many years past. The Departmental traction is kept in such first-rate repair all the time that work is rarely interrupted through breakdowns, all building-work is expertly supervised, blacksmithing and more delicate metal work is carried out on the spot, the three departmental carpenters are supervised and important suggestions in connection with the tsetse fly traps are made and incorporated. Continual calls are met from every member of the staff. Mr. Rosch carries out also most of the Department's photography.

(d) Natives in charge of investigations.

Swedi Abdallah, head fly boy in the Department since 1920, has since 1921 regularly carried out surveys for months together without supervision and has been given many other responsible tasks. His work, checked over by European officers, has in every case proved absolutely thorough and reliable, and his energy and his knowledge of the various tsetses is great. Lent to the Sleeping Sickness Officer for most of 1922 and used for the detection of sleeping sickness cases, in those days carefully hidden, he distinguished himself there also. Threatened by spearmen, he meekly accompanied them as far as their chief, and there—gave them in charge. Following up a difficult case in which the relatives of the sick man kept moving the latter from one part of the district to another in order to avoid the sleuth, Swedi finally overtook him just after death and still, despite threats, took his blood-smears. It was to Swedi that the identity of what was then the undescribed fly, which was subsequently described as *G. swynnertoni*, was first referred by officers in Mwanza in 1922, and who, unlike the European investigators before him, declared it to be totally distinct from *G. morsitans*. It was he who made the discovery that deciduous thicket was a barrier to *G. morsitans*. He replaced Milambo (on leave) for some months

on Maboko Island most capably. Swedi has been selected by His Excellency the Governor for the award of the native decoration—the Certificate of Honour and Badge.

Milambo Kazila has been in the Department since 1921 and has proved equal to the most responsible positions. He also was lent to the Sleeping Sickness Officer for a long period, and equally proved his value there. For three years past he has been in sole charge, with two fly boys under him, of the investigation and trapping of *G. palpalis* on Maboko Island. His weekly work consists of clearing the traps daily and keeping and listing all captures, trap by trap, date by date; of fly rounds as well on two days, including hunger-staging of the flies, pupa-searches on two days, repair of traps on one. He keeps very detailed and fairly complicated records and, visited unexpectedly at considerable intervals, is always found up to date and reliable. The deductions from the data, naturally, are made by a trained European entomologist, nor will it be possible finally to round off Milambo's work without the intervention of an entomologist. These reservations would apply to any native, but the fact remains that Swedi, Milambo and Yusufu are successfully doing work that is commonly done by a European assistant. Milambo has been awarded the Jubilee Medal.

Yusufu Kasandala has done highly skilled and responsible work, particularly in the handling of the parasite *Syntomosphyrum.* Doing largely laboratory work, he has always been in a station in which there was a European officer, but there can be no doubt that he would have been as capable as Swedi or Milambo of taking on independent charges.

It was a native assistant, Yusufu Cheke, now dead, who, when Dr. Nash was hampered by a blowfly parasite which anticipated his infections of the pupae with the tsetse parasite *Syntomosphyrum*, carried out an experiment on his own initiative in exposing the pupae to heat and thus actually solved the difficulty.

(e) Natives in charge of stations.

In addition to Milambo and (for several months) Swedi on Maboko Island, Mohamedi Oto has been in charge of the Itundwe Station for five years past. He has not had to do scientific work but he has had to keep grass fires out of quite a considerable area, and to burn certain plots in certain months. He has done all this most successfully.

Of the natives placed in charge of large labour camps, Makashasha has particularly distinguished himself. The work of approximately three thousand five hundred natives was supervised by him, five hundred at a time, in 1934. Makashasha and Samuel were presented to, and complimented by, His Excellency the Governor in December 1934. Yusufu Cheke was similarly presented to, and complimented by, Sir Stewart Symes in 1932.

4.—ACCOMMODATION.

(a) Residential accommodation.

Old Shinyanga, previously for the most part dismantled, was turned again into a station by the repair of the old fort and the division of its single set of quarters into two, for the use of the Senior Entomologist and myself, the transference of our four small, portable wooden houses from Kikore, each a load for the Guy lorry, the rebuilding of the old agricultural house for the Assistant Director and the closing up of the old open native meeting-house (baraza) to form a house for the Senior Field Experiment Officer. Messrs. Jackson,

Wheeler and Lombard live in pole and mud camps in the bush. In general, we are very badly housed compared with any other department or investigation and the water supply is bad, but, with all too little money for the work, our members have gladly tolerated, for its sake, a considerable amount of discomfort.

(b) Scientific accommodation.

A cramped verandah in Mr. Potts's quarters formed the entomological laboratory at Shinyanga, the laboratory at Kikore having had to be abandoned as such. No herbarium existed; the plants were kept in the Botanist's and latterly in my quarters; and no accommodation was available for exhibits.

This was altered in 1934. The storerooms of the fort, which were high and spacious but lighted at the top only, have been converted into a useful (though much too small) laboratory, herbarium and museum by the enlargement downward of some of the windows and other necessary work. Money has not sufficed for all the work required and our laboratory facilities in particular are thoroughly inadequate.

PART 2.—THE INVESTIGATION OF THE HABITS AND ECOLOGY OF TSETSE FLIES AS A MEANS FOR DEVISING THEIR DESTRUCTION.

Note: Terms used in the present paper.—A list of definitions of such of the terms used in the present paper as may not be understood generally is given in appendix 1.

A.—THE BROAD LINES OF THE ATTACK.

1.—THE GENERAL SCHEME.

The original scheme of investigation was that " experimental reclamation " and " research " should go hand in hand. The former would provide points for the latter to solve, and the latter would attack the difficulties of the former as they arose and would provide information on the bionomics of the fly and hints for new or improved methods. This line of work has its empirical aspect, but it has proved highly practical, and it is a practical and urgent problem with which we are dealing. It has equally been scientific; for the rôle of the scientific staff, in addition to studying closely the bionomics of the flies, in both the laboratory and the field, for suggestions as to control measures, is to keep all the field experiments, and in some cases, as at Marialuguru (p. 366), even interesting tribal attacks on the tsetse, under close, continuous, and critical, observation by the methods to be described on pp. 32–42.

The measures which the department adopts pass through the following phases:—

(a) *Scientific observation and experiment.* In the course of the study of the flies an observation is made or an experimental result is obtained which suggests an idea for the fly's destruction.

(b) *Initial experimentation* is then carried out to test the reasonableness of the idea.

(c) *Field-scale experimentation.* Even if the measure shows promise, we cannot yet recommend it, for we do not know what difficulties may arise when it is applied on a large scale. The measure is therefore next tested on a field scale and the attendant difficulties appreciated. These are then either overcome, or proved so to detract from the utility of the measure as to lead to its abandonment.

(d) *Trial, or consideration, under more widely varying conditions,* gives us the scope of the measure.

The brief histories of some of our measures given, *e.g.* on p. 241 and pp. 294–296 bring out these points.

The following can be said of the system as employed hitherto:—

(i) The work is carefully and logically planned on scientific lines.

(ii) Our field experiments are closely watched from start to finish by trained scientific men; all observable and recordable factors are taken into account, and every change in the density and even condition of the fly is fully noted, within the acknowledged limitations of our steadily-improving technique.

(iii) Controls are duly provided.

(iv) The largest field experiments are, therefore, just as much scientific research as the smallest experiments carried out in the laboratory, except that

their interpretation is more difficult, since the natural factors encountered cannot be isolated and controlled like the artificial factors used in the laboratory.

(v) This makes laboratory work also essential, though much can be deduced in the field from regularly repeated association of apparent cause and effect. The laboratory work itself has severe limitations and its results should not be accepted unless confirmed in the field. More laboratory work is, however, needed—and is in hand—in order to obtain a fuller understanding of the mass of observations that we possess on tsetse behaviour in the field and, for example, on the effect on the flies of our own non-grass-burning experiment. Meantime the observations have been made and we know now what it is that we need to explain. Meantime also the effect of not burning—both on the vegetation and the flies—is before us, and the necessary position is available for study for the improvement of the measure.

(vi) Without these large field tests it is impossible in any case to say whether a suggested measure will in practice be useful or useless and how to carry it out.

(vii) Some of these tests have had the effect already of reclaiming much land for the natives and have thus, in a practical fashion, been paying their way. From 1924 to 1934, inclusive, approximately 700 square miles of country were reclaimed or added to grazing, partly by ourselves, partly by others following up our initiative in the matter.

(viii) The conditions under which we have worked—demand for immediate results, coupled with complete uncertainty of continuance for much more than one year ahead—have naturally precluded the use of more long-range methods.

2.—TEAM WORK IN ATTACKING THE TSETSE PROBLEMS.

Team work has been kept prominent throughout. On investigating (whether for information or with a view to intelligent attack) a piece of infested (or possibly infestable) country, the first thing demanded is a botanical survey; for the distribution, density, and reactions of the flies depend first on the local "eco-climates," with separate opportunities for feeding, sheltering and breeding, with which differing vegetation provides them. A knowledge of the distribution of these is essential. A coincident or subsequent entomological survey indicates the actual presence or absence of flies, reveals their feeding-grounds, breeding-grounds and "homes," and throws light on the composition of the population and its state of nourishment. A game survey—regarding the amount, kinds and distribution of the foods of the fly—is also necessary.

With all this before us, and with the knowledge that we have gained already by scientific team-work of the ways of the particular tsetse concerned, we can study our local problem and plan our experimental or practical attack. Before this can begin, it is necessary to obtain an estimate by an experienced field-experiment officer of the labour requirement and cost of the experiment or of the measures which, on the strength of other surveys, it is desired to undertake. This officer usually takes charge of the operation—either completely, or, if it is carried out by the administration and tribe, at least as regards technical supervision.

Although each member of the staff has botanical knowledge and both the Botanist and Mr. Harrison, either of whom is called in for the more minute botanical surveys, have a good knowledge of tsetse flies, it is commonly found that an experiment of any size or importance can best be handled by team work. Accordingly, whenever possible, the work is divided between botanists, entomologists, game-men and the executive. It is impossible to

send the whole team to each tribal problem, but a visit by an entomologist as well as by the executive officer concerned is arranged for when necessary and possible.

The head office plays an important part in the team-work, for, as stated already, it relieves the less distant officers in the field of all accounting and clerical work.

B.—TECHNIQUE.

The following sub-sections describe how our surveys are made, how a knowledge of the density, condition and composition of the fly population from place to place helps us, and how these are ascertained.

1.—METHODS OF BOTANICAL SURVEY.

Note: Some of the maps attached to the present paper (maps 1, 2, 4, *and* 6) *and all the aerial photographs illustrate methods of botanical survey.*

(a) Sketching of vegetation distribution from the air.

The sketching of vegetation distribution from the air is productive of rapid results but without high accuracy. That part of map 6 which lies west of the Rift Valley is by Burtt. It deals with 5000 square miles and was compiled entirely from notes and sketches made during four long flights in an aeroplane. It gives a good general idea of the distribution of the five leading types of country—dense thicket, "miombo" (*Isoberlinia–Brachystegia*) wooding, thorn-bush (mainly of *Acacia rovumae*), seasonally swampy grass-land, and the interzonal wooding of *Combretum*, etc., that divides the miombo from this grass-land. A more accurate map made by this method is that of the vegetation round Kazikazi (pl. 20, fig. 2). For choice of sites for an experimental measure, or as a preparation for attack on or defence against the tsetse, this method is invaluable. It needs to be followed by ground-work in sites selected from the air. In its simplest form this kind of survey consists merely of notes made on air reconnaissance. This has also been very valuable.

(b) Primary survey.

Survey is made of the different main plant communities either on foot or by car. This is the " primary survey " of the plant ecologist and an example of the result is shown in map 4 made by Nash of his area round Kikore. A map of this type is an essential preliminary to any study of the tsetse or, in key sites chosen from the air by method (*a*), to an attack on them.

(c) Detailed mapping of the exact interspersal of the various vegetational elements.

A necessary preliminary here is the division of the block into squares. This is done by means of path-transects carried through the bush, north to south and east to west, with the aid of a prismatic compass and pole, a measuring wheel and a small gang with axes and hoes. Our unit was to have been one of 1000 yards a side, but as a matter of convenience and practicability this has been doubled in the case of Block 9 at Shinyanga and halved in that of 10A (fig. 5).

Still using the compass and wheel and with the transects as base lines subdivided further by pegs, the distribution and forms of the various patches of the different vegetational communities is plotted on squared paper on a scale of 5 cms. per 100 yards. The density of the vegetation is at the same

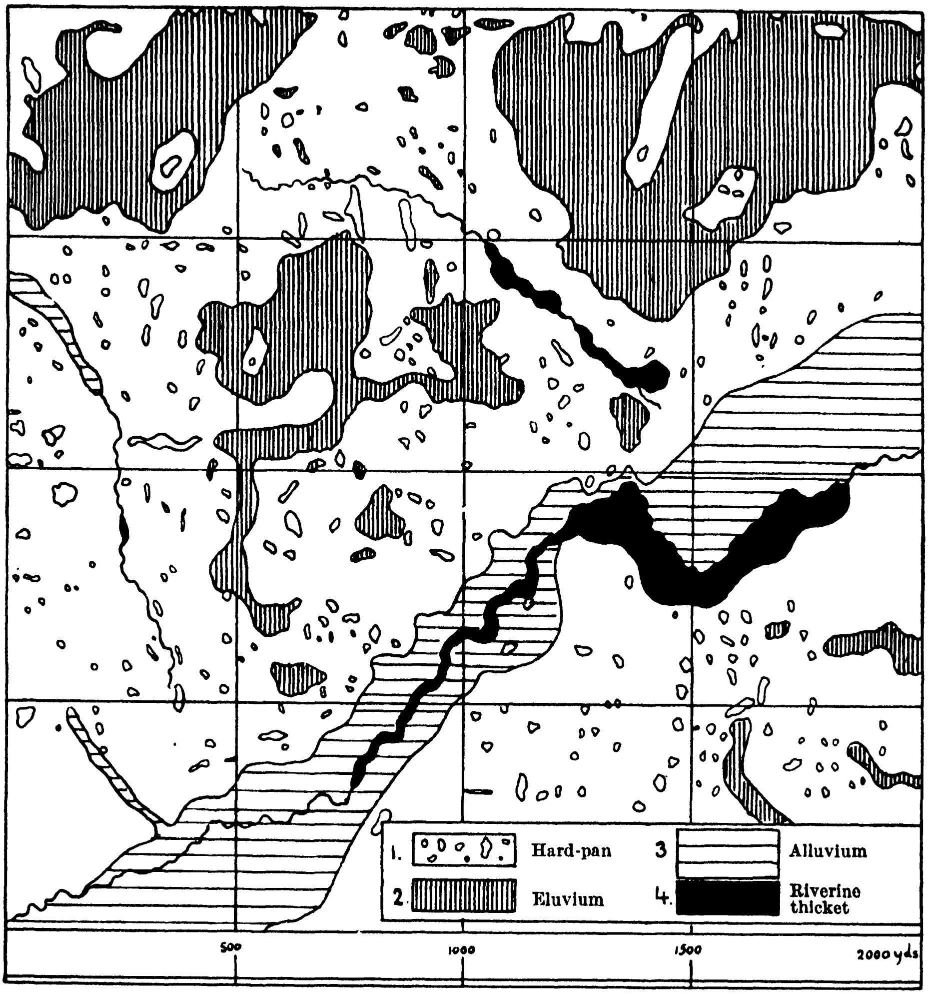


FIG. 5.—One square, 2,000 yards to the side, showing the main vegetation types, carefully charted, from Harrison's map of Block 9 at Shinyanga. Even the small thickets are shown.

time rapidly and approximately recorded, the following rough but useful scale, suggested by Burtt, being used :—

D. 1. Impenetrable thicket, necessitating the cutting of a path.
D. 2. Thicket penetrable without the cutting of a path.
D. 3. Still so thick that a compass traverse is impossible without cutting a path, grass covering commonly about 10 per cent.
D. 4. Visibility still better, grass covering about 20 per cent.
D. 5. Easy to traverse with a compass, grass 30–50 per cent.
D. 6. Grass-land exceeding ground covered by bush.
D. 7. Scattered trees in otherwise open grass-land.
D. 8. Open grass-land.

In practice, for categories D. 4–D. 7, depth of visibility in yards provides a more suitable description.

This method is of great value when one has either to study the exact relations of animals to their vegetational surroundings, to plan detailed discriminative clearing, or to record plant succession, *e.g.*, in response to not burning.

(d) **" Quadrat-type " survey.**

In the case of one half-square in Block 10A, Burtt has attempted to record the position, species and height of every tree and separately standing shrub. This, repeated several years hence, will give a very close picture of the successional changes that will have been brought about by not burning the grass.

Still closer quadrat-work was carried out by Scott under Phillips in our plots in Kikore in 1929 in several vegetational communities, the individual plants being staked, numbered and recorded. The plots still stand unburned for examination with their burned controls.

(e) **Photographic surveys, vertical and oblique, from the air.**

Many of the illustrations in the present paper are taken from the survey, vertical and oblique, that was carried out in Shinyanga in 1931 and 1932. This stands as a detailed record of the vegetation at that time of about 80 square miles of country, including much country since (i) kept unburned, (ii) burned with special intensity, (iii) burned merely native fashion.

This method gives us a record of the original condition and a close measurement of changes in the country, revealing details that will help us to plan our work and attain our object in country in which we are conducting research or control. Owing to its expense, the vertical method is applicable only to " key " sites which have been selected by visual aerial reconnaissance. The method described under (a) above, amplified by obliques, suffices for the bulk of the country.

2.—ENTOMOLOGICAL TECHNIQUE (FLY CENSUS).

It is important, in what amounts to a study of the population dynamics of the tsetse flies, to be able to compute the density of the flies and the proportion in which examples of each sex occur or appear to us, and, similarly, the proportions of young and old flies. It is only by means of density computations carried out week by week over a period of several years that we have gained an accurate knowledge of the reactions of the flies to the seasons and to varying weather conditions, to the different types of vegetation, and to the movements and density of game. It is only by similar computations that we are able to gauge the effect of our measures on the flies and to separate this effect from that of the seasons, weather, game-movements and other extraneous influences and say either, " We are being successful," or, " This treatment won't do." The proportions in which females appear to an observer are an indication of hunger and of the presence of feeding-grounds (many females appearing) and of breeding-grounds (few). From the numbers of the young flies, the strength of emergence and the presence of feeding-grounds may be deduced.

Inter-specific density is deducible, but less accurately, owing to the greater unwillingness of certain species of tsetse to come to man. This can be remedied to some extent by the use of bait-cattle. In practice it is most conveniently met by the use of " bait screens " (pl. 10, figs. 2 and 3, and p. 243 below).

The following are some of the methods by which a fly census has been attempted :—

(a) Flies per boy per hour.

The index to density afforded by the number of flies that will come to a stationary catcher with a net in one hour was employed by Carpenter (1912, 1919) and Fiske (1920) and has long been in use. It is specially useful in observations carried out to test the movement or drift of the flies that are in or visiting a site.

(b) The fly round.

The fly round, a method devised by Potts in November 1927, has been an improvement on this, for general ecological purposes, for all the " land " flies and, actually, for *G. palpalis* as well. In this method a track is laid out by means of blazed trees which traverses, so far as possible in their due proportions, the various local types of country. The round is divided into numbered sections, each of which corresponds with a vegetational type, the number being painted on a tree at the point of entry into it. The fly boys conducting the traverse stop every twenty yards or so to capture all flies settling on themselves and on the ground round them. The flies captured in each section are separately tubed, and separately examined and analysed as regards density, sex, age and hunger—these last two diagnoses at least being carried out at the time of capture. In this way types of vegetation that are blanks or partial blanks as regards tsetse are separated from the rest. By comparison of the sectional results and by sufficient repetition, a clear picture is obtained of the relative suitability to the fly species concerned of each type and sub-type of country, and of the " economic density " of the tsetse species in relation to each, at all seasons and under all conditions. The density in each section throughout the year is studied to ascertain seasonal mortalities, bursts of increase and other fluctuations, and to deduce their causes. The whole round or rounds (giving " lowest density " Elton, 1933 : 51) and sections (giving " economic density ") in one block of country are compared with those in another and with those of the control block (4B in Shinyanga), in order to deduce relative success—on the fly's part and on ours. In Kikore the regular fly rounds were kept up for 4½ years; in Shinyanga they have been running for nearly 5½ years.

(c) The fly reconnaissance.

The fly reconnaissance is a variant of the fly round in which a single track is not repeatedly followed. It is used in sampling new country or parts of the area under study or attack in which lack of staff forbids regular fly rounds. The procedure is the same, the flies for each vegetational type and each game density (where noted) being separately considered.

(d) Car reconnaissance.

Car reconnaissance has been defined by Jackson as follows :—

" Roughly speaking, it is found that over a given distance a car attracts about as many flies as a party on foot collecting by routine methods, although the car takes more females and fewer males. A party collecting on foot progresses approximately 2 miles an hour through thin fly (under 10 per mile). This may help to give some idea of the meaning of flies taken on car reconnaissances. The method is to proceed at about 12–20 m.p.h., and to catch only while moving. Two or three catchers in an empty lorry are normally adequate. Flies are called out according to sex as they are caught, and recorded. The passage of tenths of a mile, and broad changes of vegetation types, etc., are recorded, through dictation by the European who is driving. The method is

practicable with a loaded lorry also, provided that fly is not too thick. In thick fly there is delay in keeping the car clear."

The object of car reconnaissance is to discover the broad distribution of tsetse on very large areas rather than to relate it to changing vegetational types.

(e) Flies per boy per 100 yards.

Nash invented the method of flies per boy per 100 yards, which is a further improvement on old methods, giving us equalisation of area. "Since the length of the fly-round paths is known, one has the two constants: distance and number of catchers. Fly density, as expressed by this F.B.Y. (flies per boy yard) unit, can readily be obtained from the following formula :—

$$\frac{\text{No. of fly}}{\text{No. of boys} \times \text{distance}} = \text{F.B.Y.}$$

In practice it has been found that the result works out at an inconveniently small figure, so it is multiplied by a hundred, making the unit "flies per 100 yards" (Nash, 1933).

Actually, we are at the moment finding it best to make the distance unit 10,000 yards, particularly in order to get a direct comparison with the game figures which are commonly not worth recording over even 1000 yards, though this last figure may in the long run prove best.

(f) The use of bait-cattle, screens, and traps.

(i) *Bait-cattle.*

Early in my prior work * I found that *G. pallidipes* and *G. brevipalpis* could not usually be attracted in sufficient numbers to make their study worth while without the use of bait-cattle. This was owing to their relative dislike of man. In one area I observed *G. brevipalpis* all the time coming towards me and turning back if cattle were absent. I found also that in these species and in *G. morsitans* an approach to equality in the sexes, or in special cases a female preponderance, was obtained when cattle were present, but that, when cattle were not present, practically only males could be caught. Moggridge has reported of *G. pallidipes* in Kwale "a large number of the flies were caught . . . only after prolonged spooring with the aid of the sound made by their short flights." How great a difference the use of bait-cattle may make may be judged from the following tabulation of the totals of the flies taken by Wallace near Amani in one month (30th April to 31st May, 1926) :—

	G. pallidipes.	*G. austeni.*	*G. brevipalpis.*
On man . . .	2	1	5
Using bait-cattle . .	16	420	942
Total taken	18	421	947

It will be noted that without bait-cattle the microbiologist would have taken few flies in the course of a month's work.

At the same time, cattle, varying as they do both in attractiveness and in tractability, do not form a good standard of measurement, except in so far as the same individual animals can be continuously used.

* Swynnerton, 1921.

(ii) *Bait-screens.*

Screens of sacking or cloth (pl. 7, fig. 1) were first used by myself to attract flies in 1922. From 1931 onwards, following close experimentation by Jackson and Herbert Lloyd, they were used on fly rounds and reconnaissances for *G. pallidipes*. "T" screens (pl. 10, fig. 2) are now regularly used on the rounds in Block 9, on reconnaissances elsewhere and for all work on *G. pallidipes*. How useful they are in this connection may be deduced from the following extract from Potts's report for 1933 :—

(iii) *Comparison of screens with hand catches off man.*

From February to October regular catches with screens have been carried out along the rounds in Blocks 4A and 4B, with the following results :—

Block.	No. of rounds.	*G. pallidipes* per 10 rounds.	Female %.	Young flies %.	Total caught.
4A Fly boys only.	36	1·7	33·3	16·7	6
4A Screens.	26	21·9	40·4	26·3	57
4B Fly boys only.	31	5·5	16·7	22·2	17
4B Screens.	24	55·0	32·3	19·6	133
					213

From these figures it would appear :—

(i) that the number of *G. pallidipes* caught is greatly increased by the use of screens;

(ii) that the percentage of females is increased markedly, but that the percentage of young flies is not raised so much.

(iv) *Comparison of screens with bait-cattle.*

Out of the 18 specimens of *G. pallidipes* taken by Wallace in Amani, 87·5 per cent. came to the bait-cattle and out of a hundred taken by Burtt in the dry season near Mpapwa, 87·7 per cent. came to the bait-cattle, while out of the 213 taken on Potts's comparative rounds 89 per cent. came to the screens. This actual comparison, striking as the coincidence looks, may not be worth much; but, generally, the catch off screens compares reasonably with that made on cattle and is at least high enough to make it a useful method of studying "density activity." Screens are much simpler than animals to handle and catch from and they eliminate the strong individual variation of the latter, though that of the fly boys remains.

Each screen is carried between two fly boys and the enumeration of the flies is "per screen."

It should be noted that in catches off man, screen and cattle, the flies are also caught and included which settle on man or the ground.

(v) *Traps.*

For the species for which they are useful at all, traps produce captures which may be compared to the standing catch of the old "flies per boy-hour" method, but include far more females.

"It has been found that traps designed to catch only hungry flies will catch about 50 per cent. of females [*morsitans*] even in the 'home.' . . . The same was found to apply to *G. swynnertoni*, when this species was being trapped experimentally in its 'home' in January 1931. At this time and place, about 50 flies an hour could be caught with nets (mean hunger stage 2·6 to 3·0) of which only about 1 per cent. were females, but of flies caught in the traps the females were over 50 per cent." (Jackson, 1933*c* : 456). With *G. pallidipes* and *G. palpalis* far higher female percentages are caught.

In our experience with *G. pallidipes* it has been rare for a trap to catch well continuously in one spot, though it is realised that Harris's traps in Zululand, with a much heavier population of this trappable fly, have done so. The slump that has occurred with us after a really heavy day's catch is remarkable.

Generally speaking, any hope that traps could be used by themselves as continuous indicators of fly density and composition has been disappointed. A fly round has been necessary also.

(g) The "fly-grid."

The "fly-grid" method of measuring density, worked out by Phillips and described in detail by Potts (1930) was also designed for the comparison of the fly density obtaining in different vegetational communities. It aimed at taking only the flies that were present on the site of the catch and eager to attack. Reluctant flies and flies probably arriving from a distance were largely eliminated by limiting the catch at each site to a period of 5 minutes. The catching party had eventually to be made six in number, to be able to deal promptly enough with the flies when these were numerous.

"On approaching the site of the catch the flies on the party were caught, bottled and (later on), released and the party appeared on the scene from behind a screen to prevent the flies destined to be caught from coming to them too soon. During the catch, movement by the catchers took place at the end of each two minutes to and fro to a spot 10 yards distant, the movement contributing extra attraction; but it was found that this flattened the grass and thus probably unduly attracted flies to the spot. A 'grid' was therefore laid out at each catching site. Working its several bars and different portions of them in turn, the same ground was traversed only once in six days. The time of day at which the catches were made was constant. It was hoped to obtain from these 'ecological catches' the response of the fly to the variable factors within the environmental complex, these factors being :—daily and seasonal changes in the floral community, in the faunal community, in the fly itself, and in the physical factors" (Potts, 1930). The catches were made beside the meteorological station in each community.

(h) The "recovery index."

Jackson, in June 1930, invented and in November 1933 (1933*a*) published the following method of computing the fly population of an area. A fly round, tapping as fully and uniformly as possible the area concerned, is carried out. All the flies captured on this round are at once marked and released. On subsequent days recapturing is carried out indiscriminately through the marking area. The number of marked flies recaptured, and that of new flies caught on these repetitions, are noted. The total population bears the proportion to the total of the flies that were marked that the total number of flies captured bear to the marked flies recaptured. This method has been tested in

various places and, allowance being made for deaths and a fair margin of error, is giving useful results.

We have lately found that this simple and ingenious method is not new, having been used successfully already on a great scale for water-fowl computation by F. C. Lincoln in the United States (Lincoln, 1930, quoted by Leopold, 1934—the "Lincoln index"); but to Jackson belongs at least the credit of having devised it independently. Actually we can claim originality for most of our present field methods. For greater detail, see appendix 1.

It may be added here that fly populations are being measured for comparative purposes in unconfined areas also. Thus in the *morsitans* experimental area in South Tabora "a rectangle, approximately square, has been indicated by a hoed path, marked out with the aid of a compass, entirely enclosing the Kakoma round. In this rectangle flies are marked twice weekly on consecutive days (Thursday and Friday) to show date of marking. From these figures it will be possible to compute at short intervals the population of old males in the rectangle and, by comparison with fly-round figures, to determine what factors activate *G. morsitans*. So far it would seem that there are between one and two thousand old males in the rectangle, which is about two square miles in area" (Jackson). It has proved possible to allow for dispersal.

(i) Measurement of the composition of the fly population appearing.

That the composition of the capture—females per cent. and young flies per cent.—is of the greatest importance in helping to determine the conditions and the use to which the fly is putting a particular spot, has been adequately stressed already. This measurement is used by us very extensively whatever method of capture is adopted.

Standing or "drift" catches are useful for the diagnosis of the flies' use of a spot. In a feeding-ground after the first rush of flies, a smaller but fairly steady supply of arrivals continues to come in indefinitely, or to drift past the observer. In the "home" few flies come after the first rush is over; the population within range of the fly's senses of detection is exhausted and there is afterwards no regular arrival or passage.

(j) Measurement of the condition of flies.

Jackson has paid much attention since 1927 to the measurement of the condition of flies and has evolved a definition of the chief stages of hunger on which it is possible, by rapid examination in the field, to secure agreement by separate observers, including trained natives, to within a 14 per cent. error. This may be reduced for practical purposes to about 3 per cent. by border-line cases being treated as cancelling each other out. The relative hunger of the flies has been a most important indication of distress, of well-being, of imminent falls in density, of the factors that cause them, of the steps which we might take to add to the distress, and of the season at which to take them. It is also a useful corrective: the great reduction of the fly population of Block 4A in a period of not burning the grass might well have been credited to reduced visibility, causing failure to find food animals, if the continued repletion of the surviving flies had not shown that some other factor must be sought.

(i) *Technique of hunger-staging.*
(pl. 21.)

Owing to the fact that in tsetse flies the fat-bodies become maximally developed shortly after ingestion of a meal of blood, and thereafter decrease

rapidly to a small volume before the really hungry stage is reached, it is possible to judge from the external appearance of flies the approximate stage to which digestion has proceeded. If in addition the length of the hunger-cycle (period from feed to feed) for the particular time and locality is known, it is possible to estimate how many days have elapsed since the last meal, and how many are likely to supervene before the next one is specially sought for. This would not be possible if the tsetse retained well-developed fat-bodies for long after digestion had ceased. Owing to the complication of pregnancy in the female tsetse, the stage of digestion cannot be gauged from the external appearance in this sex. The present classification is as follows :—

Stage I : Gorged.
Stage II : Replete.
Stage III : Intermediate.
Stage IV : Hungry.
Y : Young flies, which have not yet had their first meal.

The following is a simplified description of these stages, excluding young flies, which have never yet fed and are recognisable by being quite soft :—

If a fly is diagnosed correctly as stage I or stage II, the abdomen must be neither wrinkled nor concave ventrally, nor must it be straw-coloured; and it must be two-thirds or more opaque when held to the light.

A fly correctly diagnosed as stage IV must be definitely concave or flattened, with the underside of the abdomen straw-coloured, yellow when held to the light.

Any fly which does not fit either of the above descriptions, and is therefore intermediate between the two, is assigned to stage III.

Flies fitting the first description, and also showing red or blue-black blood from the outside, are assigned to stage I.

In practice stage I flies are neglected, on the ground that, though now gorged with blood, they have very lately been hungry, and tend to remain in the same locality as the hungry flies for some time. after the meal. Their numbers in ordinary samples are in any case small. Females are neglected. Young flies also are excluded from the estimate, since although they are certainly hungry their numbers must be strongly affected by the emergence rate, which varies with the season.

The mean hunger stage [M.H.S.] of the remaining male flies (stages II, III and IV) is found by multiplying the number in stage II by 2, the number in stage III by 3, and the number in stage IV by 4. The sum of the products is divided by the total number of flies in these three stages contained in the sample. The calculation should be worked to two places of decimals. Thus :—

Males :	I	II	III	IV	Y	Females : Mature	Y
	5	23	85	18	1	3	2

$$\text{M.H.S.} = \frac{2 \times 23 + 3 \times 85 + 4 \times 18}{23 + 85 + 18} = 2{\cdot}17$$

Males :	I	II	III	IV	Y	Females : Mature	Y
	0	0	5	10	4	12	3

$$\text{M.H.S.} = \frac{2 \times 0 + 3 \times 5 + 4 \times 10}{0 + 5 + 10} = 3{\cdot}67$$

The great advantage of this method is that the meaning is conveyed at sight, the possible values for the estimate varying from 2·00 to 4·00 with hungrier values above 3·00 and repleter values below it (Jackson, 1933*c* : 448). The averages are taken to two places of decimals, but naturally only the wider differences are taken seriously when making comparisons.

Nash (letter to Swynnerton, 18.vii.1933) noted that, in order to deal expeditiously with great numbers of flies and further eliminate the personal factor, he had, for his own use, modified Jackson's hunger-staging as follows :—

> I have retained Jackson's grade I—gorged—and his grade IV—hungry; stages II and III I have telescoped into one.
>
> Thus I only recognise three stages :—
>
> I. Gorged fly.
> All recently fed fly that contain red or black blood, when looked at externally.
>
> II. Starved fly.
> All fly showing those obvious symptoms of excessive hunger—wafer-like, yellow abdomen, flattened and often very concave, etc., etc.
>
> III. Intermediate.
> All fly that are neither in grade I nor II.

Actually, special tests have shown that differences due to the personal factor are not great in practice, if due care is exercised. We all find that Jackson's hunger-staging method works well in practice and is exceedingly informative. The stages have been duly correlated with the internal condition of the flies.

(ii) *Diagnosis of hunger by means of fly behaviour.*

Two standards are used by Jackson to diagnose hunger by fly behaviour. These are (i) whether the flies on persons, screens and animals settle head up or head down, (ii) the proportion between those that settle on the ground around the person and those that settle on him. It has been found that the inclination of the fly to settle on the catchers or on the ground or vegetation is associated with the state of hunger of the fly, and further that hungrier individuals will usually sit head-upwards and replete flies head-downwards when settling on the catchers.

Stage I (gorged) and II (replete).

Flies in these stages seldom attack the catchers, preferring to settle on the ground. Those in stage I that do alight on the catchers may assume either the head-up or the head-down position; those in stage II usually rest head-downwards. These stages do not attempt to feed on man.

Stage III : Intermediate.

When alighting on man, flies in this stage may settle either head-up or head-down, but most prefer to settle on the ground. They will sometimes feed on man.

Stages IV and Y. Hungry and young flies.

Hungry and young flies seldom settle on the ground, preferring to attack the catchers. They alight on man nearly always head-upwards, and most are willing to feed.

TABLE 2.

Hunger and behaviour of flies in different communities (*G. morsitans*).
(Jackson, 1933 *b*.)

Fly community.	Fly condition.	Mean hunger stage.	Percentage mature males on ground.
Home	Replete	2·4	90
,,	,,	2·5	90
,,	,,	2·6	90
,,	,,	2·7	90
,,	,,	2·8	85
,,	,,	2·9	80
,,	,,	3·0	80
Mixed	Slightly hungry	3·1	75
,,	,, ,,	3·2	70
Feeding-ground	Rather hungry	3·3	60
,, ,,	,, ,,	3·4	50
,, ,,	Hungry	3·5	40
,, ,,	,,	3·6	30
,, ,,	,,	3·7	20
Open feeding-ground	Very hungry	3·8	10
,, ,,	,, ,,	3·9	0
,, ,,	,, ,,	4·0	0

(k) Measurement of the movements of flies.

Jackson must, up to date, have marked nearly 30,000 flies with a view to throwing light on their movements. The results are referred to on p. 196 below, and the methods of marking are discussed on p. 41 below.

In the first year in Shinyanga and again now in Blocks 9 and 10A routine marking has taken place on the fly rounds. It has been useful in each case in revealing movements from one block to another and imperfections in the barriers against fly passage.

(l) Measurement of the weight of flies.

Differences in weight, denoting the prevalence at the moment of larger or smaller individuals, is proving of use. This is different from the measurement of "condition," and in practice the two can be distinguished.

Young wild flies in December averaged less in weight (16·5 mg.) than young flies (17·6 mg.) collected during July–August. In itself, the difference is small, but a similar and even greater difference was observed at all hunger stages in the flies collected during these two periods, so that there may be some significance in it. It is suggested by Potts and Jackson that the July–August series may be the product of a more favourable period than those of the December series. This (*a*) supports the general conception, based on more indirect lines of evidence, that the late dry season constitutes a hard time for tsetse flies; and (*b*) possibly provides an additional standard by which to judge of the occurrence of other hard times. Buxton and Lewis's observations are referred to on pp. 192 and 193 below.

The observation and inference is in accord with Sir Guy Marshall's observations in about 1899 on the difference in weight of the seasonal forms of the species of the butterfly genus *Precis* Hübner, the larvae that fed in the dry season giving rise to the smaller wet-season form.

(m) Technique of marking flies.

FIG. 6.—Searching for pupae and marking flies on the edge of a *G. swynnertoni* concentrating-ground. The figure on the left of the central group, Swedi Abdallah, head fly boy, is marking the flies brought him by the two small boys on the right, while the native in the centre is entering the details of each fly in a notebook. Limonite rock and hard-pan in the foreground, eluvial-type thicket behind, with *Commiphora ugogensis* and climbing *Combretum longispicatum* in leaf on the left and *Commiphora Eminii* further right.

Lamborn (1915*a*) and Carpenter marked tsetse flies by snipping off a portion of a tarsus.

In October 1909 I used ordinary artist's oil-colours for marking experiments on butterflies (Swynnerton, 1915). Fifteen years ago I found (Swynnerton, 1921) that the snipping of the tarsus of a tsetse fly was unreliable owing to the fact that natives, catching tsetses by a foot with the edge of a knife-blade, sometimes break a piece off. Attack by a bird might produce the same effect. I therefore used water-colours from tubes,* a small spot being densely applied for the marking of tsetse flies in order to ascertain their movements. This enabled me in some cases to recognise individuals again and again and the conspicuousness of the marks brought me reports from the natives as to the spots at which such flies reappeared. It doubtless also carried with it the disadvantage of laying the flies open to destruction by birds (Swynnerton, 1920).

This system has been much elaborated by us since and the following methods have been used :—

Nash employed blanco, tinted, in an experiment in November 1927, to ascertain whether young flies wandered further than old. Paint was not available. He also (in 1929) used marked flies in an experiment to determine

* Oil-colours being unavailable.

the sense used in search of food (Nash, 1930, and p. 204 of the present paper).

Scott in 1929 (*S. Afr. J. Sci.*, **28**: 372) devised a system of marking with oil-paints, afterwards regularly used in Kikore, which showed, on the fly's recapture, the place, date, time of marking (morning or afternoon) and condition of fly when marked. Plate 21, and the explanation thereto, should be consulted in this connection.

Scott first ascertained by experiment that the paints we use are not deleterious to the flies.

Jackson devised a system which gives the same information as Scott's but not the time of day. It has advantages in allowing for re-marking on recapture, and in making flies marked on any day easily recognisable by the catchers. Combinations of two colours, varied daily, are used. Four positions in the centre of the thorax are marked, variation in the colour arrangement of which gives the place of capture and condition of the fly. In addition peripheral positions are utilised clockwise all round the thorax. In these the date of recapture is given by the combination of colours for that date and all other information by the original marking combined with the position of the peripheral marks on the "clock face" (pl. 21). At Kakoma the date and weight are recorded on the flies. Eleven colours are used in all, and marking is done with two colours at a time. Differential markings are available to cover a period of six months.

This clock system in its simple form was employed usefully by my son (B. S.) and by myself in the New Forest in the summer of 1933 in an attempt to estimate (*a*) the movements, and (*b*), by the "recovery index," the population of a small colony of the grasshopper, *Chorthippus parallelus* (Zetterstedt). Eight positions were used round the thorax, "12 o'clock" being reserved for the week, which was shown by different colours, and the other seven (of one colour) for the days of the week. The central area was used to record other information. By varying the colours weekly for the days "12 o'clock" could have been made available also for the recording of additional information. Re-marking was possible also (pl. 21).

In the experiment on butterflies, referred to above, the underside of the hind-wings was used. There being more room here, a number was painted on a small patch from which the scales were first rubbed. This, with the notes taken, was sufficient for the study of the movements of the insects. In addition eye-spots and other markings, variously placed, were used to test their effect in drawing or deterring attack by birds. In marking tsetses, it has been found that a very fine wood spindle, used instead of a brush, gives the neatest results. Its end, dipped in paint, is placed sideways over the point on the thorax to be marked and the spindle is slightly twirled. A piece of board, bored into from one edge to hold small glass tubes, is attached to the belt or hung over the shoulder and in these corked tubes are the paints, ready mixed to the right consistency.

Whether the method can be trusted to indicate the longevity as well as the movements of the flies is uncertain without some knowledge of the extent to which a conspicuous marking may increase loss through enemies. Jackson's results in this connection are in each case very consistent, but we have seldom had anything approaching the lengths of life which Carpenter was able to record through the method of snipping the tarsus, *i.e.* periods ranging from 247 to 253 days for a male and up to 182 days for a female.*

* See also footnote on p. 47.

3.—MEASUREMENT OF THE DENSITY AND MOVEMENTS OF GAME.

(a) Measurement by direct enumeration.

Direct enumeration has so far been our method for measuring the density and movements of game, except for the small antelopes. Each block in Shinyanga in which a detailed game census has taken place has been divided by narrow path-transects into squares—as described on p. 30 above.* This applies to Blocks 4A, 4B, 9 and the "tens." Block 11 (less detailed survey) has merely been divided into thirteen convenient divisions by means of existing paths and internal fire-breaks.

Every transect is fully traversed by a scout at least once in three days and reports of game seen and fresh spoor (of other herds) brought in. The European Ranger's own spoor has to be reported by the scouts as a check on their own movements. In Blocks 9 and 10A each resident party and herd of the more conspicuous animals is, it is believed, known already by its composition or some special feature, and the density per square or square mile or length of transect at different times of the year can be computed. In 4A and 4B (dealt with on pp. 272—275 below) we are also approaching this position.

Births and disappearances are noted, as are immigrants and emigrants, and movements to water. The movements from day to day are represented, as stated on p. 288 below, by a line of a different colour on a ground-plan representing the squares. The relative mobility of species and herds also thus comes to light. The results of the fly rounds are correlated with those of the game rounds, and both are correlated with phenological observations on the vegetation. The meteorological observations at headquarters, not far away, are available also.†

(b) Measurement by sampling.

In the case of the smallest antelopes (dikdik, steinbuck, duiker) and hares that take cover readily and cannot be seen at a distance, estimation by "sampling" has begun to be carried out; a drive through four squares revealed an average of so many dikdiks per square (see p. 289) and the ratio between this and the average number of dikdiks seen on the rounds is being used pending a closer drive in the shortest-grassed season of the year. The average "effective strip" will be very different for duikers from what it will be for the dikdiks. In the more open country the larger species of game at least can be identified and roughly enumerated from the air.

It may here be remarked that the recording of game density in Africa has hitherto been very unsatisfactory. Such indefinite terms as "common" and "scarce" have invariably been used and it has been frequent for a man with small experience to call game "abundant" which others would call very moderate in amount. It is suggested that the game seen per mile, with an estimate of the average depth of vision from the route followed—that is, of the "effective strip"—would be a useful standard to adopt on safari or reconnaissance. Spoor would be used as the indicator when the game is nocturnal.

4.—ECO-CLIMATES AND THEIR MEASUREMENT.

The climate of a locality, as measured in the usual fashion by means of instruments placed in and beside a Stevenson screen in a spot completely open, is its "general" or "standard" climate. This is, however, by no means the

* See figs. 5 and 7.

† See also fig. 7 (on p. 44).

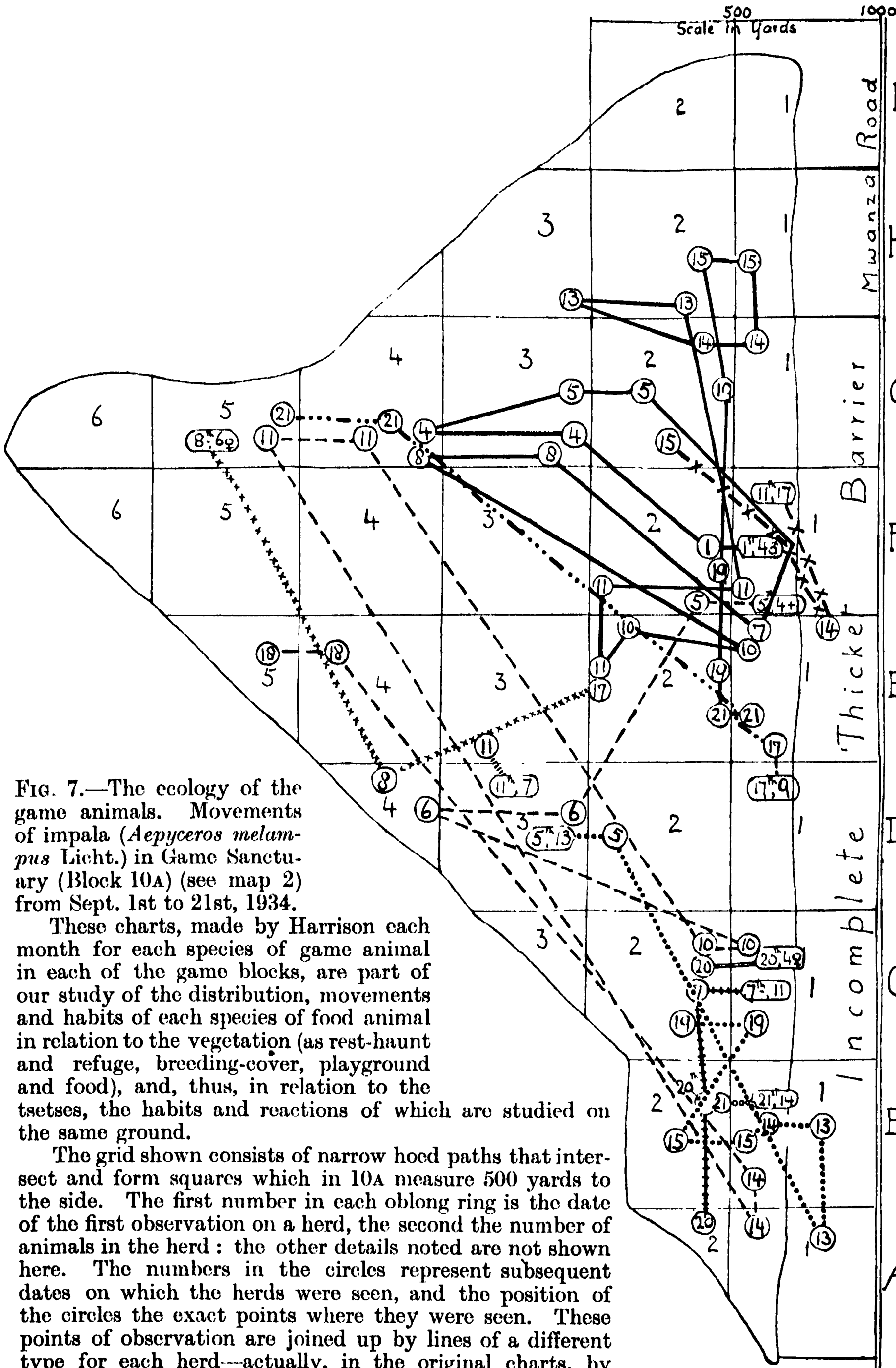


FIG. 7.—The ecology of the game animals. Movements of impala (*Aepyceros melampus* Licht.) in Game Sanctuary (Block 10A) (see map 2) from Sept. 1st to 21st, 1934.

These charts, made by Harrison each month for each species of game animal in each of the game blocks, are part of our study of the distribution, movements and habits of each species of food animal in relation to the vegetation (as rest-haunt and refuge, breeding-cover, playground and food), and, thus, in relation to the tsetses, the habits and reactions of which are studied on the same ground.

The grid shown consists of narrow hoed paths that intersect and form squares which in 10A measure 500 yards to the side. The first number in each oblong ring is the date of the first observation on a herd, the second the number of animals in the herd : the other details noted are not shown here. The numbers in the circles represent subsequent dates on which the herds were seen, and the position of the circles the exact points where they were seen. These points of observation are joined up by lines of a different type for each herd—actually, in the original charts, by lines of a different colour.

The vegetation of the block falls into the " dry thorn-bush " category. It has been charted in considerable detail on the lines shown in fig. 5.

climate that is experienced by a tsetse fly. The fly spends a proportion of its time in the sunlight, moving in search of game, or on a man or a game animal, and varies even this procedure by passing resting spells in shady places which vary from the shaded side of a tree to the centre of a dense bush, each offering quite different conditions. When resting the females at any rate hide in nooks that are even darker, cooler and damper, such as the grooves of bark, or rot-holes, or the under surface of logs just raised off the ground. These nooks, again, in the case of many of the flies, are in thicket, but in the case of *G. morsitans* in savanna wooding—and the climate in each case is different. The climate of the sunlit feeding-ground, of the man's naked perspiring back, of the thicket, whether rest-haunt or breeding-ground, and of the grooves, rot-holes and log undersides, is in each case very different from the climate which we normally measure. The conditions offered by any of these situations constitute an eco-climate—or the climate of the home of the tsetse fly, or of part of it. But the hole, groove, or log, each has an eco-climate which is different, again, from the eco-climate of the general thicket or general savanna wooding in which the flies seek and find them. One needs badly a subsidiary term for these very constricted " eco-climates " in nooks. " Micro-climate," which has been applied to them, has been used also as a general synonym for eco-climate and, as others* have pointed out, is not a good word. " Ecidio-climate " is the term suggested by me here and will be used in the present paper. It is derived from the Greek *οἰκίδιον*, a small house, and is an accurate diminutive of eco-climate.

An eco-climate can be modified by the hand of man. If we once know the conditions of temperature, humidity, radiation, etc., which can, and cannot, be borne by the species of tsetse which we are attacking, we can thin its thickets or otherwise modify its climate to the point at which it must leave or die. The measurement of eco-climates is therefore important if it is combined with investigation of the tsetse's limits of tolerance.

The measurement of the eco-climates of a thicket is relatively easy, as bulky instruments can be used. Moreau (1935) used recording thermohygrographs in screens. Buxton and Lewis (1934), in Nigeria, used maximum and minimum thermometers, a thermohygrograph in a screen, and a soil thermometer. The ecidio-climate of a groove or rot-hole is much more difficult to determine and the smaller it is the more difficult is the problem. Buxton, who has done pioneer work on this subject, discusses appliances in some of his publications (1931 and 1934). In one of his papers (1934*a*) he has described a paper hygrometer for the measurement of the humidity of the air in small and inaccessible places without disturbing the air. " It consists of a small piece of thin writing-paper, about 1·5 sq. cm. in area, weighing 10 mgm. This piece of paper has a hole at one end, and can be hung on a torsion balance and weighed." With this " humidity can be measured accurately to 2 per cent." Dew-point apparatus is useful for certain types of situation.

For the temperature of small nooks, the thermo-electric method represented by the thermocouple may be the best, though small-bulbed mercury thermometers have been usefully employed for this purpose.

In our own more recent attempts we have been handicapped by the lack of appropriate apparatus and of the money to purchase it. We have used whirling and Assmann hygrometers and Livingston atmometers in the measurement of our larger eco-climates. Herbert Lloyd noted that : " Readings are being taken with a whirl hygrometer at five feet and with an Assmann hygrometer at eighteen inches simultaneously. At the same time the wind force is measured

* Shaw, 1929; Kirkpatrick, 1935.

with a Biram air meter at five feet. . . . In spite of the fact that the Assmann hygrometer draws air through it other than the air that it displaces it was able to show that the air at eighteen inches is more humid than that at five feet. These readings also showed that more humid conditions existed in the thicket at both levels than outside."

In the case of Blocks 4A and 4B "twenty-four points have been taken in each block in various types of bush where readings are taken with the instruments mentioned above. In addition readings are taken at two points in the thicket barrier, at two points on the Mantini road and at one point in the regenerated clearing in Block 4A. At seven of these points in each block maximum and minimum temperature readings are taken with Six's maximum and minimum thermometers. Three atmometers have been placed in each block, one in eluvial vegetation, one in hard-pan vegetation and the other in alluvial thicket. It is desirable to put more atmometers out in the various types of vegetation, but at present the apparatus is not available. A thermo-hygrograph will also be placed in each block, in hard-pan vegetation, when available" (Lloyd).

Since it is impossible to take readings simultaneously in each block, a definite round is followed and reversed on the following day. Four rounds constitute a series of readings. On the first day the round is done as described above. The next day the round is reversed. On the third and fourth days the rounds are started three miles along, in each block. This ensures that readings are taken at various hours of the day at each point in each block.

Each set of readings is the mean of four rounds. Fly-catches accompany the readings.

5.—REDUCTION OF ERROR.

In the fly-round method it is usual to carry out the fly rounds in pairs, on successive days or with an interval of one day, whether this is done once each week, once in ten days or at wider intervals. This tends to correct the activity irregularities that occur from one day to another. In addition, the round is done from a different end on each of these two days in order that by doing each section at a different hour of the day we may even out so far as possible the errors which would otherwise arise. The results, for each section, of the two pairs of rounds are averaged or computed together. The rounds (when the flies are killed) are not conducted more often for fear of unduly reducing the fly population in the neighbourhood.

The same number of catchers are used each time and they are dressed exactly alike, though this is not possible where sheer attack by large numbers, as opposed to investigation, is in hand (see pl. 10, fig. 3). I was once criticised for dressing our natives in khaki on the ground that it savoured of militarism. The answer was easy—khaki colour is attractive to the tsetse and standardisation is vital.

Differences in catching ability can be disregarded, since the fly boys quickly become very expert and most of the flies give repeated chances. Fiske found that different fly boys tended to catch different proportions of females. We have never noticed this with our fly boys, possibly because two always catch together, so that the chemotropic influence of one is possibly offset by that of the other, and because all are trained to catch similarly.

Conspicuous marking of the flies is of immense advantage. On the other hand, as stated on p. 41 above, it is not known to what extent it increases mortality through enemies with resultant vitiation of the longevity-estimation experi-

ments. The conspicuous paint markings on the wings of butterflies which have been referred to above definitely drew attacks to those markings while the insects were resting, as was shown by the fact that the subsequent damage by the beaks of birds usually involved both wings. Tsetses are, however, more active and wary during their daylight rests than are butterflies.*

Females and young flies are left out of the general density count, as they vary too greatly (the females especially) in the incidence of their appearance to man. Our density counts are based on old males.

The width of the "effective strip" on either side of the transect from which flies are drained by the walkers necessarily varies from point to point with the density of the lower vegetation and the consequent range of vision. As old males only are used for the density count and these frequent the more open savanna wooding, this variation probably does not greatly affect our general results. But it is definitely a vitiating factor and the subordinate sections of the rounds are therefore selected for relative density amongst their other characteristics.

The width of the "effective strip" in the game observations is for the larger animals undoubtedly on the average very much greater than that of the strip from which the tsetses come to the walkers. This produces the illusion in the figures for certain blocks in which flies are plentiful, that game-animals are as common as the flies. This can only be corrected by ascertaining and averaging for every section of transect the range of human vision and, for the flies, the range from which they detect and come (*a*) to man, (*b*) to a screen, and (*c*) to bait-cattle under varying conditions. In Shinyanga the total number of sections on the fly rounds alone is 157, so that it seems best here to ascertain roughly the fly population at intervals in the more important blocks by means of the "recovery index." In the case of the game of open, short-grassed plains, like the Serengeti, the difficulties are less great, but in Blocks 9 and 10A, with tree and shrub cover and grass that for much of the year is fairly long, different distance allowance has to be made (*a*) for the larger animals with conspicuous coloration and habits, and (*b*) for such small animals as dikdik, duiker, steinbuck and hare (which, in addition, often lie motionless).

The possibility of extending the "recovery index" method to the game animals by marking with missiles carrying paint or capturing, marking and releasing, has been discussed with a view to testing its usefulness in these blocks of known populations of certain species. Something in this direction will be attempted later.

Despite the employment of all the methods described above for the elimination of error, the activity of the flies or their readiness to appear to man, cattle, or screens, varies with their hunger and with the weather conditions. All therefore that we measure on the ordinary fly rounds is the "density activity." Actually, as will have been seen above, we are able to-day to make considerable allowance for the most important variable, *i.e.* for activity, by noting the condition of the flies caught, the composition of the catch, and the behaviour of the flies which compose the latter. We are finding, in practice, that the fly rounds afford a useful general comparative index to density, and Jackson has evolved a method for arriving at true-density estimation (appendix 3). To get a complete and fully accurate picture of any situation, we must take out separately true density, activity, rates of larviposition, emergence,

* Moreover, since the above was written, Jackson has put the matter to the test by trying out conspicuous markings against inconspicuous ones on male flies. The difference in the proportion of the conspicuous and inconspicuous flies recaptured was negligible.

death, and diffusion, and then correlate them with the changes in the physical and biotic factors. "It is still true that these conditions themselves are complex and cannot be separated except in the laboratory, but, backed by laboratory work, we can take a very long step forward if we separate the components of fly behaviour in the field" (Jackson, letter to Swynnerton). In any case, as Potts (1930) observes, "any body of data allowing the correlation of environmental factors with the numbers of fly caught must be of direct utility—(*a*) in assessing the value of variations in the physical environmental factors as influencing activity, and thus obscuring true density, and (*b*) in showing whether activity may be influenced by some factors (other than the physical environmental factors) at present unrecognised, and needing to be elucidated. This knowledge is essential to tsetse control, both in the interpretation of data obtained by short-duration reconnaissances of fly areas carried out with a view to planning their elimination, and in the assessment of the progress of such control measures when instituted."

C.—THE DISTRIBUTION OF THE MAIN PLANT AND ANIMAL COMMUNITIES, AND OF THE TSETSES IN RELATION TO THEM.

The different species of tsetse inhabit very different types of country, and also very different sub-types where they occur in the same general habitat. It is important for the planning of measures against them to be well informed on this question in order to avoid taking steps to defend country which they would never invade, and to avoid wasting time in cutting down bush which is either of no vital value to the local species or only valuable when combined with other plant communities.

1.—THE DISTRIBUTION OF THE TWO MAIN WOODLAND COMMUNITIES.

(map 1.)

The sylvan antithesis to which I would, at the outset, draw attention as decisive and indicative of the distribution, actual and potential, of some of our chief east African tsetses is that between the "nyika" or "dry thorn-bush" (*Acacia–Commiphora*–other genera—pl. 1; pl. 3, fig. 2; pl. 5, figs. 1, 2; pl. 13, and pl. 14, fig. 1), in its numerous forms and combinations, and the "miombo" wooding (*Isoberlinia–Brachystegia*–other genera—fig. 8, pl. 11, pl. 3, fig. 1). Each is described more fully in sub-sections E and F, dealing with *G. morsitans* and *G. swynnertoni* respectively.

The nyika, occupying a great part of the Sudan and Somaliland, sweeps down into Tanganyika through Kenya and Uganda, but is arrested by impact with two masses of miombo that form the northernmost extensions of a wood of this composition and sub-continental dimensions. Displaced by smaller areas of thorn-bush or, in the eastern Congo especially, by areas of rain-forest, miombo from here southward to about the Tropic of Capricorn is the form of wooding that probably gives their main character to the several territories concerned. There is much miombo in the eastern Belgian Congo and Southern Rhodesia, while Nyasaland, Portuguese East Africa, and Northern Rhodesia are essentially miombo countries.

The western of the two great miombo masses referred to above begins in the Biharamulo district, widens to its full extent (300 miles) on the Central Railway, and then swings south and west to the Northern Rhodesian border. Except for four tongues yet uninfested, in the Mkalama, Singida, Kondoa–

Irangi, and Dodoma districts respectively,* it also forms the great western fly belt of Tanganyika Territory, comprising 90,000 square miles.

The great eastern miombo fly belt comes in on almost the whole width of our contact with Portuguese territory, withdraws in a deep bay round Songea and thence, first following the Usongo escarpment, runs generally on a course that is rather north of north-east. It just embraces Mpapwa in its margins and (as a block of moderate solidity) terminates near Handeni. Outliers continue, however, further north to a point at the back of Mombasa.

FIG. 8.—Miombo wooding (*Isoberlinia–Brachystegia*–other genera), with the grass burned off.

The eastern belt contains much more wooding that is not miombo than does the western belt. There are large areas of miombo itself, of *Acacia pallens* and *A. usambarensis*, of *Ostryoderris–A. pallens*, of *Sterculia appendiculata* and thicket, of drier thicket, with succulents and *Terminalia spinosa*, of heavy closed forest on the large rivers of Mahenge and on the Usongo scarp, and of what can only be called " coastal debris." The latter, flanking the coast in varying depth, consists of old Arab coconut plantations, many in use, others abandoned as the result of the abolition of the slave-trade, sisal plantations, well-weeded or full of thicket, and native cultivation closely dotted with mangoes, cashews and *Albizzia Lebbek* that has been allowed to run wild. It comprises in addition the secondary thicket and savanna communities—much-hacked *Pteleopsis* and miombo on the sandstone, less molested *Hyphaene*-palms on the clay—which abandonment of cultivation has allowed to regenerate or which cultivation has spared. The thicket, with (in parts) much secondary *Phyllanthus*, is in some areas largely evergreen, with climbing *Landolphia* rubber, *Uvaria*, *Gymnosporia*, etc. In other parts (as on the rift-scarp behind Dar-es-Salaam) it is of a finer,

* See map 1.

more varied, and forest-like form, with " mvule " (*Chlorophora excelsa*) and a tall *Albizzia* of the *sassa* type, but containing also *Landolphia* and *Uvaria*, and may represent what the lower thickets were before the bulk of their component species were exterminated locally by man. Most of the whole is infested, but cattle are kept (unaccountably sometimes) in certain coast sections.

The great southern tongue of the dry thorn-bush or nyika is wedged into the mouth of the opening between these two great blocks consisting (mainly or largely) of miombo. This broad opening, further south, in Iringa, where it is above 4,000 feet (Greenway), contains much miombo which is still uninfested. The Usambara and Pare mountains drive a wedge of rain-forest conditions into it on their tops further north. Otherwise it is interrupted mainly (in Tanganyika) by the closed forest (rain and other) on the sides of several extinct volcanoes and by some great open plains, the few trees on which are themselves of the " thorn-bush " category. A large proportion of the dry thorn-bush is infested with tsetses.

The dry thorn-bush or nyika, as here defined, is to be distinguished from the wooding, on alluvial soil, of *Acacia pallens*, *A. usambarensis*, and (on the streams) *A. albida* and *A. campylacantha*, which occur on alluvium in the miombo also, and may there be regarded as part of the miombo combination, though not of the miombo association proper. As a whole, with its three characteristic tsetses, *G. longipennis*, *G. swynnertoni* and *G. pallidipes*, the nyika occurs under, and is indicative of, much drier and more trying conditions than those associated with the miombo and *G. morsitans*. The miombo, despite the name of *Trocken-wald* or " dry-forest " given to it by the Germans and despite the fact that *e.g.* in western Singida it succeeds under conditions that definitely appear very dry—and represent the dry end of its range—is, as a general association, more mesophytic (*i.e.* more demanding of medium moisture) than is the general thorn-bush. At the wet end of its range, miombo, even with the self-same dominants, such as *Isoberlinia globiflora*, occurs beside rain forest or with rain-forest shrubs as its under-storey.

The thorn-bush, as a habitat for tsetse, is dealt with further under *G. swynnertoni* (see pp. 85–90 below).

2.—THE OTHER PLANT COMMUNITIES.

(map 1.)

The thorn-bush numbered 3 on map 1 and infested with *G. morsitans* is of the more mesophytic thorn-bush type described above as often occurring in the general miombo climate. Such are the *Acacia pallens* areas in Kilosa, Morogoro, and on the margin of the Mkata plain and the enclaves which occur there of stink-bark (*Acacia usambarensis*). A distinctive community, separated from miombo, is the *Acacia hebecladoides* association of Bukoba and southern Uganda, with old-man's beard lichen (*Usnea*) hanging from the branches, which is infested with *G. morsitans* also. This is dealt with further on p. 60 below.

No. 4 community is described briefly on pp. 59 and 86 below. No. 5 high-level community comprises two or three communities which commonly intermingle: e.g. *Protea* and *Faurea* (*speciosa* and sometimes *saligna*), *Terminalia torulosa* and *Parinarium curatellaefolium*; *Sizygium owariense* and *Uapaca* (*Kirkiana*, *Zanguebarica* and *nitida*) tend to occur with them. Bracken is often associated, but this, and the *Sizygium*, *Uapaca*, and *Parinarium*, may under special conditions also be found at sea-level.

No. 6 community (coast debris) has been referred to. No. 8, thorn-bush or nyika infested with *G. pallidipes*, is not essentially different in character from

no. 7 (infested with *G. swynnertoni*) : *G. swynnertoni* could also, it is thought, infest no. 8. No. 9, uninfested thorn-bush or nyika, is similar and mostly infestable. No. 10 includes all highland grass country, more or less open, from the grass-savanna above the miombo line (which could carry wooding, were the fierce early fires brought about by quick drying through cold to allow of it) to the tussocked and channelled alpine meadow of Kilimanjaro. Heath for convenience is included. Lower grass-lands with trees, not coming into this category, and in some places (*e.g.* in South Kavirondo) probably the result of past settlement, constitute no. 11, in which the grassy hill country, with scattered bamboo groves, of Kibondo is included. No. 12 comprises all the "climax" closed-forest types, from the mangroves of the sea-shore and the dense wooding of the shores of the lakes, to *Brachylaena*-, olive-, conifer- and rain-forest—the latter, tropical, intermediate and temperate; or, in drier country, dense deciduous thicket. Colouring no. 13 on the map represents cultivation steppe, and white (no. 14) either is vegetation unknown or lies out of the area mapped.

The drainage lines traversing the savanna may be :—

(*a*) glades (pl. 3), widening sometimes into plains (pl. 12, fig. 3);

(Either is known as "mbuga" in Tanganyika and Kenya, as "dambo" in Nyasaland and Northern Rhodesia, or as "vlei" (the Africaans word) further south. These remain more or less open as the result of overwetness in the rains, but the covering is essentially grass. Great plains (pl. 2) occur also in the volcanic and other soils of northern Tanganyika.)

(*b*) permanent swamps, closely covered with tall papyrus, reeds or (more locally) bull-rushes;

(Such are shown in the map on the Kagera north and west of Bukoba, in the Malagarasi system between Kibondo and Tabora, and on the Ugala river. They occur on the margins of the lakes, large and small, and some of the other greater rivers.)

(*c*) cut-out stream courses, some with permanent water, most without.

(These are lined for the most part with more luxuriant vegetation than occurs in the savanna which they traverse—with "riverine thicket" in the thorn-bush (pl. 4) or fringing forest more nearly of rain-forest type (fig. 16) in better rainfall areas or on streams with permanent water.)

The fringe may be wide, narrow or absent.

3.—THE NAMES USED FOR THE PLANT COMMUNITIES.

It is held that it is preferable to give to the main woodland communities names which will be understood and which can easily be learned by everybody. "Miombo" is strictly the Kiswahili name for a *Brachystegia* of the *filiformis* group—that with long, rather large but narrow leaflets close together—but the term is used everywhere in east Africa, by natives and Europeans alike, for the general type of wooding which is dominated by any of the trees of the genera *Isoberlinia* and *Brachystegia* and which contains in constant association with them numerous other genera as well. This very distinctive and widespread type of wooding has other native names elsewhere, but none of these names has anything like the range of the word "miombo." To this must be added the fact that Kiswahili is fast extending its own range. I therefore urge that the term "miombo" should be brought into general use, with the scientific synonym "*Isoberlinia–Brachystegia*–other genera" to indicate its dominant trees and its

mixed composition. In the present paper, I have used the term "formation" or "association"* respectively to indicate whether it is the country characterised generally by miombo (with other interspersion) or the miombo proper that is indicated.

The same argument can be used for the "dry thorn-bush." There is no general native name here, but the term "thorn-bush" is well known to all Europeans in east Africa for the dry thorn-bush types and is very descriptive, as well as having been used by some German writers. On the other hand, a word is in use by the Kenya natives for the dry thorn-bush which is "nyika." It has been used in the past by Roosevelt and Heller (1915) and by myself (Swynnerton, 1920). Mr. Greenway, who finds it employed in Ukamba in Tanganyika, has suggested in conversation that its use might be recommended. It has the advantage of simplicity and being a good mate for miombo, and it is convenient to have a brief collective name for what is, after all, despite its patchwork nature, one great climatic formation. "*Acacia–Commiphora*–other genera" should, it is suggested, be the general synonym. I prefer to retain this title for an association which almost everywhere combines these two dominating savanna genera, in close juxtaposition or mixed, as its most prominent features (Swynnerton 1925, quoted by Phillips, 1929: 355, as a synonym for his "deciduous scrub").

"*Combretum*" is not used as part title of either the miombo or the thorn-bush for reasons given on p. 90 below. This is mainly on account of its ubiquity.

4.—THE DISTRIBUTION OF THE VERTEBRATE FAUNA.

(map 7 and appendix 5.)

A knowledge of the distribution, both general and ecological, of the vertebrate fauna is of the greatest importance to the study and control of the tsetse flies. The preliminary work accomplished is shown on map 7 and in appendix 5.

Map 7 gives the distribution of the larger mammals, which provide the main food of the tsetses, as it was known to me early in 1929, before I relinquished the Game Wardenship. S. P. Teare, present Game Warden, who has kindly examined it carefully, states that it still holds good. Some additional detail is, however, available which I have not had an opportunity to incorporate.

In appendix 5 is given the territorial distribution of most of the larger mammals and of some of the smaller, with that of such of their races as fall within the east African countries from the Zambesi to the Sudan and Somaliland frontiers. A preliminary indication of their ecological status and their probable contact with the tsetses is also briefly attempted.

The following may be added here as regards the ecological assemblies and communities* into which the game animals fall. Each is necessarily considered (and, I suggest, best named) in relation to the plant community, or combination of plant communities, to which it is normally attached. All our work emphasises the view that an adequate and reliable study of animal ecology can be carried out only on the basis of a thorough knowledge of the plant communities and a realisation of the factors that influence the distribution of the latter. This applies to the food animals of the flies as much as to the flies themselves.

The conditions governing and supplied by our two main types of wooding, the miombo and the nyika, form combinations so different that, monopolising as these formations do large sections of the continent, their main masses may

* For the definition of these terms, see appendix 1.

be regarded as almost of sub-regional or "provincial" (Engler) value. The chief features common to the two is that both are composed of pyrophytic or fire-resistant trees and shrubs (Swynnerton, 1917) and that for the most part both are swept by the annual fires which result from, and perpetuate, the condition that the ground-cover is grass and that the wooding is without much under-storey. Each formation therefore possesses a large herbivorous ground population, both vertebrate and invertebrate, and many members of the vertebrate section graze equally through both types of country. But there are marked differences between the two.

(a) The miombo game assembly.

(map 1, colour divisions 1 and 2.)

The miombo (*Isoberlinia–Brachystegia*–other genera) is the home essentially of the Sable antelope, Lichtenstein's hartebeest and, south of the Saba Sanctuary (map 7) Sharpe's steinbuck. These species are characteristic of the miombo though not necessarily dominant in numbers. Some of the animals of the nyika and plains, such as Coke's hartebeest and the dikdik, penetrate into the miombo to considerable distances from its northern boundary. Thus Coke's hartebeest is found at Sambala (map 1), west of Kondoa, and dikdik about Tabora. In addition, several species are found throughout almost the whole both of the miombo and of the nyika. Such are zebra, eland, giraffe, duiker and the various carnivora : eland sometimes dominate in numbers. Yet further, the plains that occur in the miombo—mostly seasonally swampy grasslands, SSG on map 7—carry a plains game assembly, which is, however, less varied than that of the great plains in the nyika to the north. It consists mainly of wildebeest, oribi, zebra, and ostrich; the thickets which occur in the miombo carry thicket animals (such as the red forest duiker and, nearer the coast, the suni) and part-thicket animals such as the elephant, rhinoceros, buffalo and the greater kudu. The swamps which here and there intersperse it carry some of the animals listed in the explanation to the map in the swamp game assemblies. Roan antelope and, to a less extent, topi, both using the open plains, also use the miombo of the western half of Tanganyika, where it is interspersed with mbuga.

(b) The plains and nyika (dry thorn-bush) game assemblies.

(map 1, colour divisions 7, 8, and 9.)

The characteristic animals of the great plains are the gazelles (Grant's and Thomson's), Coke's hartebeest from the Serengeti eastward, oribi, ostrich and (west of the Rift) the topi, but the line between these and those of the nyika is not hard and fast, for the species which keep most to the plains—to which zebra may be added—also use the woodlands which border them and in which they are interspersed. The animals which most use the latter—mpala (often dominant in numbers), giraffe, common steinbuck and eland, also use the plains in varying degree. The gerenuk, the dikdik, and the lesser kudu are more normally confined to the thorn-bush. The dikdik is based on thicket, though it appears in great numbers outside it; the lesser kudu is more closely attached to its thickets; the greater kudu, which is as much based on thicket as the dikdik, is to a far greater degree a thorn-bush animal than a miombo species—though if the right interspersal is present, it may occur through great areas of miombo. Roan antelope, using thorn-bush and plain, penetrates much further east than does the topi, but it then halts, perhaps on coming in contact with the type of nyika in which oryx, gerenuk, lesser kudu, and vulturine guinea-fowl (dry nyika community) are found. It reappears just back of Bagamoyo, having, however,

omitted unexpectedly from its range the whole of the more or less mesophytic area of the eastern miombo with some good plains interspersal (map 1).

The nyika is, however, far more broken up by open spaces and plains than is the miombo, so that the plains game figure in it more freely. It also contains many more thickets of deciduous type. Its game population generally is denser than that of the miombo, except where miombo-covered hills and acacia-plains come into contact. The bird populations of the two great biomes contain very distinctive elements and the differences in insects are great also. This distinctive distribution extends largely to the tsetses as well.

(c) Other assemblies.

(map 1, colour divisions 3, 4, 5, 6, 12, and 13.)

Colour division 3 in map 1, the more mesophytic thorn-bush, is rich in game animals, for, as it often divides the miombo from nearly open mbuga, it is used by both miombo game and plains game, providing, as it does, for both a concurrence of requirements. An example of this is found on the margins of the Mkata plain near Kilosa. Neither this nor colour division 4, of which the latter contains mainly the animals which are common to the miombo and the nyika, possess, so far as is yet known, characteristic game animals of their own. Bushbuck rather specially characterise the area marked 5 on map 1 and Chanler's mountain reedbuck is found in it; otherwise it mainly holds the miombo game of its neighbourhood. Colour division 6 contains a mixture of species, including even in places Sable antelope, but the thicket animals mostly preponderate. The ubiquitous eland inhabits the open grassy slopes of the highlands, as do the reedbucks, the bushbuck and the common duiker. In the close settled cultivation steppes, odd herds of Thomson's gazelle penetrate to a fair distance (in west Usukuma) and dikdiks live under the dense hedges of *Euphorbia Tiruncalli.* An odd animal of another species occasionally wanders in but is at once surrounded by a mob and killed. The game generally has been expelled.

The various closed-forest game assemblies (colour division 12), from which I here except any inhabitants of the mangrove swamps, have many species in common, and include elephant, rhinoceros, and buffalo, though these are not confined to dense country. These closed-cover animal assemblies, those of the seasonally swampy grasslands (vlei assembly) referred to under " other plant communities " above as characteristic of the drainage lines, and those of permanent swamps and water-margins are sufficiently enumerated in the explanation to map 7 and in appendix 5.

5.—A BRIEF COMPARATIVE SKETCH OF THE DISTRIBUTION OF THE SEVERAL TSETSES IN RELATION TO FLORA AND FAUNA.

(For Tanganyika, see maps 1 and 7.)

(a) *G. morsitans* Westw. The miombo (*Isoberlinia–Brachystegia*) is essentially the home of *G. morsitans.* This species occurs in some other types of wooding, as in Uganda and Bukoba, in the Transvaal (formerly) and in portions of every intervening territory, but, speaking very generally, from Biharamulo and Handeni all the way to the Limpopo, the distribution of *G. morsitans* coincides broadly with that of the miombo and, in the south, of the mopane (*Copaifera mopane*) as well. *G. morsitans* is also essentially a " savanna game " fly, with habits adapted to finding and feeding on the game animals of the miombo (see section 4 above), and on pigs and baboons. For its distribution in Tanganyika, map 1 should be seen.

(b) *G. swynnertoni* Austen. The dry thorn-bush, or nyika, is essentially the home of *G. swynnertoni*, which infests a great proportion of the country between Shinyanga and the Kenya border and Mkalama and Arusha. For this plant-formation it takes the place, as a tsetse feeding on savanna game, which *G. morsitans* holds in the miombo. It is practically confined to Northern Tanganyika and its distribution is also shown fully in map 1.

(c) *G. pallidipes* Austen. This species, which is the most catholic fly of the genus, finds great areas to suit it in both the miombo and the nyika. Selecting in each plant community the eco-climates which conform to its needs, it is able to subsist, in general, in vegetation as diverse as are the semi-desert type, full of succulents, below the two Pare ranges, and the margins of rain-forest in Kenya, Tanganyika, and Portuguese East Africa. Its northernmost known occurrence is in Italian Somaliland, where it chooses the damp river valleys; its southernmost is in the fly belts in Zululand. It appears to occur everywhere between in conditions which it can utilise in any kind of savanna matrix, extending in some cases over huge belts. Unlike *G. morsitans* and *G. swynnertoni*, which, through their quite different requirements in the matter of the savanna itself, live apart, it overlaps all other tsetses. Using the savannas as hunting-grounds, and employing dense wooding as well, its range of food is possibly greater than that of all the other tsetses.

(d) *G. austeni* Newstead. This is the smallest of the modern tsetses (as distinguished from (possibly) two of the fossil tsetses of Colorado),* and was described first from specimens sent from Jubaland (now in Italian Somaliland) by Mr. R. P. Filleul. It has since been found in suitable spots within 150 miles of the coast from there right down to Zululand. Like *G. brevipalpis* and *G. palpalis*, it is a tsetse that is based on dense wooding, though it also seeks food outside it. Its main contact is probably with bush-pig, though buffalo and other thicket animals certainly receive its attention. It also attacks cattle-bait with some readiness but is not attracted to man. The little that is known of this fly is given in Section H below (pp. 113 and 114).

(e) *G. palpalis* Rob.-Desv. Though capable of living away from rivers and lakes where the closed forest and rich damp thicket extends continuously back from them but is not over-dense, and the food conditions are suitable, this species is a fly of the great water-systems—of the Congo and its tributaries, of the other west African rivers and of the great lakes and their affluent waters. It is usually not found far from shores and banks and, while it feeds on game animals—situtunga, buffalo, pig—and, less readily, on man, where these are readily available, its main diet is reptilian and is provided by the lizards and crocodiles which commonly abound in its haunts and the tortoises which also occur there.

(f) *G. brevipalpis* Newstead. This is one of the large brown tsetses, is associated with the denser, more evergreen types of thicket and with the margins of broken rain-forest. It appears to be missing from the great miombo-*morsitans* area of the west (see map 1), until near the shores of Lake

* Four species of fossil tsetse fly have been found in the Miocene shales of Florissant, Colorado—*G. oligocena* (Scudder), a fly larger than *G. brevipalpis*, wing-length 16 mm.; *G. veterna* Cockerell, wing-length 10·9 mm.; *G. osborni* Cockerell, wing-length 7 mm.; and *G. armatipes* Cockerell, wing-length 7·5 mm. The wing-length of *G. austeni* is 8·5 mm., and of *G. brevipalpis* 11–13·5 mm. "A million years, more or less," have elapsed since these flies lived. A theory places the disappearance of the American horse to their discredit. One of the great glaciations might have contributed to their disappearance from America. It is only certain that they are one of the many evidences of an old land junction. (References: Scudder, 1892; Cockerell, 1907, 1909 and 1916.)

Tanganyika, and it is not recorded from Northern Rhodesia. So far as is known, it occurs, however, elsewhere from Kenya right down to Zululand in situations which suit it, no matter in what type of matrix. Its special association would seem to be with bush-pig, buffalo, elephant, and other frequenters of thicket, but it is believed also to scour the savannas by moonlight and to come into contact then with a far larger variety of food-animals.

(g) *G. fuscipleuris* Austen. Mr. Lewis, Veterinary Entomologist, Nairobi, has recently shown that *G. fuscipleuris*, another of the large, dark tsetses, inhabits areas in south Kenya between Lake Victoria and Lake Natron. These are roughly shown on the map, which indicates also roughly the site of an observation made long ago by Mr. Haye, District Veterinary Officer, Arusha, regarding the occurrence of the species near Lake Natron.

(h) *G. longipennis* Corti. This, a pale large tsetse with dark spots on the thorax, is essentially a fly of the driest parts of the dry thorn-bush area—the Acacia-desert grass savanna of Shantz. It is therefore found in the broad dry band which lies behind the coast strip in Kenya and in the similar dry country of the north of the Northern Province in Tanganyika and about the foot of the two Pare ranges. These last appear to be its southernmost known localities. It has not been studied at all, but its association would seem likely to be with the rich game fauna of the thorn-savanna and plains.

D.—CONCURRENCE OF REQUIREMENTS.

(pls. 3, 4, 6, and 13.)

A fact that has emerged strikingly from our investigations is that some, and probably all, species of tsetse need more than one vegetative type, not merely seasonally, but almost daily. The changes of station are most frequent in the dry season, when hunger recurs at short intervals.

The flies need country in which to find their food (feeding-ground), country for lying up in when fed or in bad weather conditions (rest-haunt), "rendezvous" sites for the sexes (mating-ground), and country offering special conditions for the puparia (breeding-ground). They need well-drained, open wooding when the rains are severe and relative humidity approaches 100 per cent. They need denser cover when desiccation is fierce. Different species of tsetse vary in their requirements for each of these purposes, and doubtless also in appropriate humidity range. Thus we find that *G. palpalis* scours the foreshore and waters for food, while *G. morsitans* searches the glades and the edges of open mbugas; *G. brevipalpis* haunts evergreen thicket and relatively moist surroundings, while the dried-up deciduous thicket of the "hard-pan" sees *G. swynnertoni* safely through. Again, sometimes one type of vegetation is capable of serving two purposes: in the case of *G. palpalis* the breeding- and lying-up grounds may be separate, in *G. morsitans* they are commonly one, and hard-pan (see pp. 93 and 94 below), where it occurs in *G. swynnertoni* haunts, contains elements which can serve all needs. It is a question in any case whether the females do not most commonly rest in potential breeding-sites. Females of *G. morsitans*, by no means all pregnant, have several times been seen resting together under logs on the ground under which were puparia. They certainly use rot-holes in trees. In my experiments with *G. brevipalpis*, captive in a large net, the females rested under the coils of lianas, of a type under which in nature they commonly deposit their larvae.

But in every case the feeding-ground, breeding-ground, and resting-ground, where they are separate, must be in fairly close juxtaposition, especially

in the hunger season, so that the tsetses may resort to each as they need it without long and dangerous wandering. Further, a locality which may combine all these desiderata at one time of the year may lack one essential at another—such as ample shade during drought, or more open country in the rains, or food-animals.

It results incidentally through this that tsetse flies are best suited along the contacts of vegetative types—or, in the case of *G. palpalis*, where water and two vegetation types meet. Leopold (1933) has discussed excellently this same characteristic for game under the title of " edge-effect " ; actually there is little that can be said of their food-animals in this respect that cannot be said of the tsetses, but, while it is the task of game management to *add* any one of these facilities which may be missing, it is the duty of the tsetse staff to remove, separate, or modify adversely one of them during one critical season of the year in the sites which the tsetse at that time is occupying. To learn to do this with a maximum of economy of effort and with a minimum of expenditure under all combinations of conditions is the chief present aim of our studies, and a further reason why discussion of vegetation figures prominently in the present paper.

E.—THE RELATION OF *GLOSSINA MORSITANS* WESTWOOD TO ITS INANIMATE ENVIRONMENT.

1.—THE VEGETATIONAL TYPES WHICH *G. MORSITANS* CANNOT INHABIT.

G. morsitans cannot live in :—

(*a*) " dry thorn-bush," as defined above, unless this be in patches and strips in the miombo, or is itself interspersed with miombo patches;

(This fly also penetrates a few miles into the thorn-bush where the latter and miombo are in contact. In the case of wooding of *Acacia spirocarpa*, *A. Benthami* and *A. Senegal*, large enclaves of these types in miombo, if involved in an advance by the flies, become surrounded by the latter and are deeply infested only gradually and, it is believed, impermanently, as the fly-density surrounding them becomes great. Where it occurs as large areas, this " dry thorn-bush " is not used by *G. morsitans*. There are certain *Acacia* woodlands as of *A. hebecladoides*, *A. pallens*, and *A. usambarensis*, which, growing under somewhat moister climatic conditions than the thorn-bush as a whole, *G. morsitans* is able to inhabit.)

(*b*) rain-forest or similar dense evergreen wooding;

(*c*) extensive deciduous closed thicket, except during the driest months, when the flies may resort to the marginal sections as a refuge from desiccation;

(*d*) open mbugas, and gall-acacia wooding in mbugas where separated by an adequate barrier from the fly bush proper * and open country generally;

(*e*) certain great areas of miombo which are evacuated seasonally by the flies or in some cases are apparently uninfested always;

(Their homogeneity—lack of vegetational interspersion—appears chiefly to distinguish these from the areas not evacuated or infested. In Southern Rhodesia it has been found that miombo on the Kalahari sand is disliked; when this is present, the flies remain down in the mopane-covered flats.)

(*f*) areas of pure *Combretum Zeyheri* and *C. apiculatum* seasonally.

Lamborn found also that in Nyasaland large areas of pure *Uapaca Kirkiana* were relatively unfriendly to *G. morsitans*.

* See pl. 12, fig. 1.

2.—THE VEGETATIONAL HABITAT OF *G. MORSITANS.*

(a) The wooding on the eluvial ground of the slopes and rises.

(i) *The miombo itself.*

(Pl. 3, fig. 1; pl. 11; and fig. 8.)

The miombo proper (*Isoberlinia–Brachystegia*–other genera) occupies the rises and slopes. It forms woods that aesthetically are very attractive during much of the year. They consist of slender trees from 30 to 60 feet high, depending on the conditions. These have small-leafed, spreading storeys of flat foliage, mostly in the upper third of the tree, and are spaced sufficiently closely to form usually a loosely interfitting canopy which, with few shrubs below, shades what is often a poor ground-stratum of grass. Various species of *Brachystegia* and *Isoberlinia globiflora* form the great majority of the trees, but among them occur species of similar habit, e.g. *Albizzia versicolor* and *A. Antunesiana*, *Burkea africana*, the fallen logs of which are one of the commonest of the tsetse breeding-sites, *Pterocarpus Bussei* (" mninga "—a good furniture timber), and white-barked *Afrormosia angolensis* (" mwanga "), large and small-leaved *Uapaca* (*Kirkiana*, *Zanguebarica*, and *nitida*), with edible fruits, and species of other genera, well distributed or in patches. Among them also are many smaller trees or shrubs, amongst which *Combretum Zeyheri* (" msana ") and *C. Fischeri* are sometimes abundant enough greatly to densify the wooding. Often thickets are present on ant-heaps, and sometimes, as in Tanga and South Tabora, tangles of the rubber-yielding lianas, *Landolphia Petersiana* and *Kirkii*, with the large-leafed but economically useless *L. florida*, form more extensive thickets both on ant-heaps and elsewhere. These, in an annually burned-back condition, sometimes cover much ground.

Westward and southward (*e.g.* in Nyasaland and the Rhodesias) *Uapaca* (*Kirkiana*, *Zanguebarica*, and *nitida*) occur freely in the miombo, but are highly gregarious, tending to form groves of their own.

Diplorhynchus, *Pterocarpus*, many Brachystegias, and some of the other genera have furrowed bark in which the resting female tsetses may hide. Hollows occur at the bases of some of the trees or in the stems. The latter in some cases lean over, and scattered over the ground there are fallen branches and trunks. These all serve the same purpose of protection from desiccation and enemies and supply in addition the shelter in which the flies larviposit. The surface soil is usually more or less sandy and the rot-holes in the tree trunks contain humus, so that the larva, full-grown when dropped, can bury itself quickly and pupate. Such a wood may cover a hundred thousand square miles, or, as in the Kikore fly belt, it may be a few miles broad only.

To an unpractised eye most grown miombo looks the same. Actually there are sub-types which differ both as between different main areas and within each area. Illustrating the former phenomenon, Jackson gives a list of 21 trees common in the miombo either in the Central Province or Southern Tabora of Tanganyika. Of these no less than 14 are absent from one of the two areas and 4 are common in one, less common or rare in the other. Only three species are common in both. The Nzega fly areas are to some extent intermediate, though nearer to that of the Central Province in the composition of their miombo. In Abercorn and parts of Nyasaland *Protea* of more than one species is abundant in the miombo; from most of the Tanganyika miombo it is absent.

In illustration of the consociations which may make up a local miombo we may take South Tabora. Here (as generally elsewhere) *Brachystegia micro-*

phylla crowns rocky crests. Where the miombo covers great areas which are nearly flat *Isoberlinia globiflora* dominates, with much *Pterocarpus Bussei, Brachystegia itoliensis* and *B.* aff. *appendiculata. B. flagristipulata,* less common here, becomes commoner as conditions transitional to mbuga are approached or, in this transitional zone, *Terminalia sericea* may be dominant. *Brachystegia Wangermeeana* ("kashishi," native name) is more definitely associated with semi-alluvial soils. Each species tends to come into leaf at a different date—the order in South Tabora being approximately *B.* aff. *appendiculata, B. itoliensis, B. glaberrima* ("mshilanga"), *B. flagristipulata, B. Wangermeeana* and *Isoberlinia globiflora.* Each, therefore, and by reason of its different sub-habitat, must play a different rôle in relation to the tsetse, *G. morsitans.*

The grass growth plays a part also. On the poor, dry, grey soils of the Central Province the miombo grass is poor or even absent. The same applies to part of Southern Rhodesia. On the soils of Handeni, Kahama, South Tabora and Abercorn it is good. In regard to South Tabora, Jackson writes: "The soils of the miombo are firm and brown, not powdery and grey like those of Central Province miombo. They scarcely erode, and support a rich grass growth, which burns off almost completely in the dry season."

(ii) Ostryoderris Stuhlmannii–Combretum Zeyheri–*other genera, on eluvial (and colluvial) soil.*

(See map 1, heading 4; and, with thickets, pl. 5, fig. 3.)

This community has been investigated by Jackson in Nzega and seems there definitely to serve *G. morsitans* as an alternative to its miombo. In a more open form and mixed with scattered *Acacia pallens* it is a less successful habitat in Handeni, mild fluctuations into and out of it appearing to occur in cycles of wet years and dry, respectively, from the permanently-infested miombo close at hand. As a plant community it covers far less country than miombo.

(iii) Protea, Faurea, *and other elements commonly associated with high elevations.*

This community, which includes also bracken, *Smilax Kraussiana, Sizygium owariense* and *Parinarium curatellaefolium*—a mixed savanna community found also in Northern and Southern Rhodesia—with *Albizzia sassa* and such Uganda elements as *Markhamia platycalyx*; much tree *Combretum* * either in groves or generally interspersed; and, on the ridges, miombo. This is found in Biharamulo and is shown as "5" on map 1. It is probable that its quite light infestation with *G. morsitans* is due to the presence of miombo close by, and on the ridges within it. A similarly constructed "inter-zone" community exists in Nyasaland, where it covers much ground and contains additionally much *Pterocarpus angolensis* and (apparently) *sericea.*

(iv) *A related, less mixed, community.*

Afrormosia angolensis and *Terminalia torulosa* are dominant in this community, with *Protea* spp., *Faurea speciosa* (in Iringa *saligna* also), much *Parinarium curatellaefolium*; and in some places groves of *Uapaca Kirkiana* and of the smaller-leaved *nitida.* This community occurs in North Kibondo and parts of Iringa Province (where *Protea* and *Uapaca* dominate). In North Kibondo it is infested with *G. morsitans,* but the same reservation applies as in the com-

* Mainly *C. Zeyheri, C. apiculatum, C. splendens,* "tree" to distinguish them from the many "rambling" Combretums (*purpureiflorum,* etc., see p. 319 and appendix 7) and the common shrub *Combretum parvifolium.*

munity described under (iii) above—the doubt, that is, whether it would shelter *G. morsitans* permanently if it were unaided by miombo.

(b) The vegetation of the alluvium.

Cutting through the eluvial wooding, miombo and other, at intervals which may be from two to five miles where the country is merely undulating and double this where it is flatter, but more frequent where it is hilly, run the drainage valleys of the land and their affluent glades. These valleys and glades form strips and interconnected basins of black alluvial soil, which are kept nearly clear of trees by sheer wetness. In this case the wetness is seasonal; in the dry season the soil cracks open and the extreme of dryness is present.

Tree first type is that afforded by the black-soil mbuga. Tree combretums (*C. ternifolium*), with large, bright-green leaves and fairly dense foliage, may occupy the damp margins, and clumps of spindly, nearly shadeless gall-acacias may be present nearer the centre. Sometimes the alluvial deposit, wet in the rains, covers so broad a site that it forms a really large enclave of open grass-country with scattered woods of these small gall-acacias.

Sometimes such alluvial enclaves, or their margins, have become drained and re-eroded into slopes. These are in effect "fossil mbugas"—to use a term of the geologists. On them grow the larger Acacias (such as *usambarensis* and *rovumae*) forming woods of their own; or, under other conditions, the drier-country tree combretums (*Zeyheri* and *apiculatum*) may form such woods and cover extensive areas on alluvium of particular types and on colluvium betwixt miombo and mbuga, as on the eastern margin of the Mkata plain.

Elsewhere on the margin of a miombo belt and especially at the foot of a scarp we may find a distribution of soils and woodland types like that of a patchwork quilt. It was this, shown in Nash's map (map 4), which made Kikore a useful site for comparative ecological study.

The following are some of the communities growing on alluvium slightly or better drained which seem, on our present knowledge, capable of forming complete habitats for *G. morsitans* :—

(1) *A. rovumae* (Mgongwa), on the drier alluvials and granite, investigated by Jackson and apparently capable, with the broad-leaved shrubs which accompany it, of harbouring *G. morsitans* permanently. It may be suspected, however, that in the climate in which this community is usually found it might, if separated from neighbouring miombo, lose its flies in an unfavourable season. Examples of *A. rovumae* wooding serving as a habitat for *G. morsitans* may be seen in an area south-east of Nzega administrative station and on the south-eastern and southern borders of the Wembere Steppe (map 1, heading 3).

(2) *Acacia pallens*, on black alluvial soils, investigated by myself on the edges of the Mkata plain near Kilosa (map 1, heading 3). Like *A. usambarensis* on similar soils this affords a complete habitat in the normal year, but a probable scene of temporary disaster to the flies in the concentrated downpours which occur at intervals of many years.

(3) *Acacia hebecladoides* (map 1, heading 3) under good rainfall in south-west Uganda and Bukoba. This is suited to permanent infestation, though a temporary "war-time" extension of a belt just south of Mbarara has receded. That the trees are festooned with "old man's beard" lichen (*Usnea*), and bananas are freely grown, shows a moisture of climate such as doubtless compensates for the more open woodland type. Thickets of *Rhus* and *Carissa* are scattered on ant-heaps through the wooding.

(4) *Copaifera mopane*, which I know in Rhodesia, occupies apparently a niche in the ecology of *G. morsitans* very similar to that of alluvial *A. pallens* above. One would have expected that this community would sometimes be very liable to the type of disaster which overtook *G. morsitans* in Kikore in April 1930.

All the above associations, where bound loosely or intimately with miombo, may be regarded collectively as forming one great vegetational formation, that of the east African mesophytic savanna, which at one end of its humidity range jostles rain-forest, and at the other end abuts on dry thorn-bush. Some of the components, as *A. rovumae* and *Ostryoderris*, here overlap from the latter formation.

3.—THE USE BY *G. MORSITANS* OF THE SEVERAL PLANT COMMUNITIES WHICH MAKE UP ITS VEGETATIONAL HABITAT.

(a) Introductory.

Both Jackson and Nash were led by their early observations to believe the glades and drainage basins (mbugas) to be "feeding-grounds," and to Jackson fell the opportunity of carrying out the special investigation by which, step by step, he proved that they were places to which hungry flies came to feed, rather than places in which flies became hungry. This investigation has been described by Jackson (1930, *Bull. ent. Res.*, **21** : 491–527) and by myself in my annual report for 1930 (: 27), and the deduction has been confirmed and re-confirmed in subsequent years by the observations of all of us in our contacts with the flies.

On this point Jackson has written :—

"Until the onset of hunger the tsetse lives and moves about in the general woodland which is its permanent haunt, and where alone it is able to breed. The general woodland is therefore termed the 'home.' With the onset of hunger every few days, the fly, unless it chances to meet with an animal in the home, sets out for the feeding-grounds, where it is more likely to meet with game. The feeding-grounds, which are to be compared to restaurants rather than hotels, since the tsetse cannot live permanently in them, vary a good deal from place to place. They are characterised usually by better visibility than is found in the home; they occupy drainage valleys or larger open spaces, often with permanent water; and they are characterised by frequent passage of game animals at least for part of the year."

Thus a piece of country infested with *G. morsitans* is divisible at any time into (i) the species' rest-haunt, which is usually also (ii) its breeding-ground, the combination being known as its "home," and (iii) its feeding-grounds.

(b) The rest-haunt of *G. morsitans* which is commonly also its breeding-ground.

The rest-haunt of *G. morsitans* is usually on well-drained ground which carries wooding of *Brachystegia–Isoberlinia* or of one of the equivalent types listed on pp. 58—60 above, but it may also be on alluvium. Thus the *Acacia pallens* community of the western Mkata plain south of Kilosa was typically divisible into rest-haunts and feeding-grounds, and the *A. usambarensis* on alluvial soil at Kikore presented the conditions of the "home."

(c) The furniture of the breeding-ground and rest-haunt.

The great bulk of the breeding-sites are usually scattered through the rest-haunt. Some of these have been listed incidentally already on p. 58.

above, but a particularly favoured site, not included, consists of extensive rock-outcrops in which many of the rocks show an overhang. *G. morsitans* under certain conditions breeds also in thicket, as has been found by myself in Buhungukira, by Jackson in Tabora, and by J. K. Chorley in Southern Rhodesia. In other cases also the breeding-sites, which are commonest in the rest-haunt and are themselves used for resting in, are not necessarily conterminous with it, for shaded ant-heaps scattered over the face of a feeding-ground may yield great numbers of puparia, as may suitable sites beside stream-courses. Further, great rocky outcrops, such as those just referred to, may be primarily breeding-ground and only secondarily rest-haunts. There is also indirect evidence—*e.g.* the finding by Jackson of only the equivalent of 245 pupae when there should (on other evidence) have been fully 3,000—to suggest that many of the pupae are scattered about and not placed in the " classical " sites. This would still be on the eluvial and a result of Lloyd's suggests that under leaf-carpet shaded by a high leaf canopy most might survive. Nooks in the bark (Lamborn, Swynnerton) may be added to the rest-haunt " furniture " which the flies have been seen to utilise.

In the rest-haunt and breeding-ground combined, the females hardly appear to man. Nash reported that in his *Brachystegia* area " during four years 55,000 tsetse have been caught . . . and only 2% were females. Yet these areas, which are the true habitats, serve as the major breeding-grounds of the whole [narrow] fly belt, and, judging from the numbers of puparia deposited, there must be large numbers of females secluded within these woods. Large collections of puparia thence show that 53% of emergences are females " (Nash, 1933, *Bull. ent. Res.*, **24** : 144). The flies which appear in such places to man are mainly the loitering and unhungry males which merely come to find females. A " standing catch " carried out in the home soon exhausts the flies coming to the catchers, thus showing that little movement takes place.

(d) The feeding-grounds.

The different types of *morsitans* feeding-ground were listed in my annual report for 1930. They may be recapitulated briefly as follows :—

(i) well-defined feeding-grounds on sections of paths or glades or mbuga-edges or passes between thickets, etc.—places where man or game must pass or tend to pass regularly (pl. 3, fig. 1B).

(ii) " spread " feeding-grounds not essentially different in function from (i), but differing through the fact that they are larger in relation to the rest-haunts which they serve (pl. 3, fig. 2D).

(iii) situations in which the fly population tends to spend all its time in its feeding-grounds, if these happen to provide the requisite conditions.

The *morsitans* feeding-grounds of this type so far seen have been very small or narrow with the typical bush of the home coming right down to, or into, them. The impression gained is that they act as feeding-grounds but that the numbers of females, young flies, and hungry males normally characterising feeding-grounds are swamped here by the numerous well-fed males which are also present out of the home just alongside. Kilosa has provided instances for *G. morsitans* and the situation is a common one in country occupied by *G. swynnertoni* and *G. palpalis*.

Normally, in *G. morsitans*, the males loitering to accost females are found in the rest-haunt, not in the feeding-grounds, but an instance in which the feeding-grounds were thus used is recorded on p. 83 below. Occasionally females have been found in these " male clusters." In addition, paths and

pieces of bare ground are frequented for the same purpose. The males travel great distances on the backs of men, on vehicles and on animals, flying off and accosting all flies which appear till they find a female.

(e) The relative extent to which different types of country appear to be utilised by *G. morsitans*.

(i) *The evidence from the density of the fly population appearing.*

The results obtained by Nash in regard to the density of the fly population appearing were quoted in my annual report for 1930 (: 25). They were based on one year's work. His results from four years' work show the same order of utilisation. This, based on the average number of flies caught per 10,000 yards per fly round throughout the four years, is as follows :—

Brachystegia microphylla, 560 flies;
Acacia usambarensis, 230;
Isoberlinia globiflora, 180;
Tree *Combretum–Terminalia* savanna, 180;
A. spirocarpa, 70;
A. campylacantha and *A. xanthophloea*, surrounding a moist thicket, 40;
clearings round settlement, 30;
open " mbuga " with a few gall-acacias, 30;
gall-acacias thickened by *A. Senegal* or *Commiphora* spp., 20;
cultivation in the fly belt, 4.

(ii) *The evidence from the composition of the fly population appearing.*

Nash's analysis of the composition of the fly population appearing, as disclosed by the figures amassed in his four years' work (representing in all 200,000 *G. morsitans*), shows further that the female and young fly percentages of the whole catch which appeared in the various woodland types stood in the following order :—

open " mbuga " (with a few gall-acacias), females 35%; young flies 32%;
clearings and cultivation, 28% and 32%;
roads, 20% and 27%;
Acacia spirocarpa, 18% and 19%;
A. usambarensis, 16% and 15%;
thick tree *Combretum–Terminalia* wooding, 13% and 15%;
Isoberlinia globiflora wooding, 10% and 14%;
Brachystegia microphylla, 2% and 6%.

The first three types form definite feeding-grounds, the last the chief rest-haunt and breeding-ground, while the *Isoberlinia*, hard by, would quite likely have shown lower figures, if (as is more normal) it had not had to compete with *B. microphylla* and the most suitable breeding-places (in the *microphylla*) ever seen by any of us in any locality. It must be remembered that *B. microphylla* covers probably not more than 0·1% of the ground in the normal *G. morsitans* fly belt, while *Isoberlinia* with the Brachystegias of the *Boehmii* and *Randii* types covers quite 90%. The remaining communities listed are transitional in their utilisation by the tsetse, or even in part substitutional for the *Isoberlinia*, except those on alluvium (e.g. *A. usambarensis*) in times of great downpour of rain.

It will be noted that the order is exactly the reverse of that which obtains for fly density. When the female percentage " appears abnormally low, one can be almost certain that the females are really abundant and that

there is much breeding in the area; when the female percentage is high there will be no females remaining inactive in the area and no puparia will be found" (Nash). The female percentage of the freshly emerged fly is considered to give a closer indication of the proportion existing in the area. "The female percentage among young fly is uniformly high (32% of the total) on all rounds, whereas among old flies it is low" (5% of the total).

Young flies are scarcest in the *Brachystegia microphylla* and *Isoberlinia* breeding-grounds, where they emerge; but they are abundant in the open mbugas and on roads. Nearly one-third of the total flies caught in the feeding-grounds are young flies, proof that the young flies, searching for their first meal, are always excessively hungry and on emerging drift to the feeding-grounds (Nash, 1930; Jackson, 1930; Nash, 1933*a*). The female and young fly percentages vary as the attractiveness of the vegetation through which they pass. The percentages are higher on the road than in the surrounding vegetation, especially the young fly percentage (though the general fly density is, at Kikore, lower on roads). It is safe to say that there is a concentration of young flies along roads.

Most of the pregnant females were taken in the transitional types of wooding between home and feeding-ground. These facts suggest that the pregnant female that comes to man is unwilling to go far afield for food and that she prefers to hunt in the tree-Combretum and *Acacia usambarensis* wooding that border the breeding-area whither she may be forced to return at short notice for the extrusion of her larva (Nash, 1933).

It is certain, generally, then, that the "cruising-radius" and the "area of search" of the female is on the average lower than that of the male and that this must somewhat immobilise the species in the matter of dispersal.

The much lower density of the flies in the feeding-ground than in the home suggests that many feeds must be obtained in the latter. But allowing for a 4 to 11 days' hunger-cycle, from 3 to 10 times more flies should in any case be taken in the home than in the feeding-grounds.

4.—THE PHYSICAL FACTORS OF THE ENVIRONMENT OF *G. MORSITANS*.

(a) The geological and elevational habitats as indicators of physical factors.

Generally speaking, in Tanganyika, the range of the miombo, and of *G. morsitans*, is that of the granites and gneisses, where these coincide with a rainfall of from 27 to 50 inches and there are no special desiccatory soil-factors, such as exist in Shinyanga. The flies spread also over some of the alluvial areas, characterised by the more mesophytic Acacias mentioned above. Miombo and *G. morsitans* occur at sea-level, and 5,500 feet is about the upward known elevational limit of this fly in the northern half of the Tanganyika Territory, so that the temperature range is wide. Western Kondoa (Sambala) affords an instance of a very flourishing belt of *G. morsitans*, part of which lies at 5,300 feet. The temperature here falls in the dry season to within a degree or two of freezing.

The soils are grey or light-red and usually very sandy on the granite; red and more compact on the gneiss, though often still sandy on the surface—and therefore easy for the larva to bury in.

(b) The standard climate of *G. morsitans*.

It should be noted that a knowledge of the range of the standard or general climates under which a fly exists merely shows (i) what degree of cold the fly will withstand, and (ii) (with laboratory knowledge of the temperatures and humidities which are harmful) the temperatures, humidities, and saturation

deficits which the fly must circumvent by betaking itself when necessary to the different eco-climates provided by vegetation, rock, situation generally, and aspect. The maxima of temperature and the maxima and minima of humidity with their periods of duration are for the most part more important than the mean temperatures. We know from Potts's experiments (p. 187 below) and the conditions under which *G. morsitans* exists in Southern Rhodesia that tsetses can withstand a high degree of cold, and from the general experiments described on pp. 177–195 below that high and low humidities and temperatures by themselves or in particular combinations have harmful or beneficial effects on particular species of tsetses.

A knowledge of the eco-climates available—*i.e.* the climates of the refuges which may protect the flies from the extremes of the physical factors—is really much more important than a knowledge of the "standard" climates.

The following tables, which give the temperature and humidity figures for Kikore over a period of four years, are taken from Nash (1933*a* : 110) and Scott (1934 : 182).

TABLE 3.

Temperatures (Fahrenheit) from thermometers in Stevenson's screens in the standard ecological stations at Kikore, Tanganyika Territory.
(Absolute maxima and minima, from Scott.)

Month	Absolute maxima		Absolute minima		Absolute range	
	1929/30	1930/31	1929/30	1930/31	1929/30	1930/31
July	81·75	82·50	40·00	38·50	41·75	44·00
August	86·25	83·00	39·50	41·00	46·75	42·00
September	88·25	88·00	48·00	46·75	40·25	41·25
October	90·25	92·00	52·00	47·50	38·25	44·50
November	91·75	95·75	53·00	51·00	38·75	44·75
December	91·75	90·00	56·50	52·50	40·25	37·50
January	91·75	91·00	54·75	52·00	37·00	39·00
February	85·50	92·25	56·00	51·25	29·50	41·00
March	84·75	85·50	59·00	57·25	25·75	28·25
April	84·75	—	59·00	—	25·75	—
May	85·50	—	53·75	—	31·75	—
June	80·75	—	42·00	—	38·75	—

The data in the following tables (tables 4, 5, and 6) are quoted from Nash :—

TABLE 4.

Mean monthly maximum and minimum temperatures (Fahrenheit) at Kikore Entomological Station, Tanganyika Territory.

Month	Mean monthly maximum				Mean monthly minimum			
	1928/29	1929/30	1930/31	1931/32	1928/29	1929/30	1930/31	1931/32
September	—	83·22	81·96	82·43	—	57·44	57·65	57·98
October	—	87·35	84·44	82·35	—	60·83	59·82	56·14
November	—	87·26	85·24	88·57	—	63·02	63·58	61·98
December	—	84·86	85·50	81·11	—	63·06	62·23	63·37
January	—	82·94	86·00	83·81	—	61·97	63·32	62·44
February	—	80·84	86·80	83·46	—	62·35	64·38	61·22
March	—	80·22	82·31	81·48	—	62·86	64·82	62·91
April	—	78·59	80·80	78·35	—	62·25	63·98	63·66
May	—	75·17	76·15	74·03	—	58·76	61·07	61·70
June	77·20	74·95	75·18	73·05	53·52	52·81	55·69	57·70
July	75·60	74·81	76·81	73·78	55·79	50·99	56·89	54·01
August	79·27	76·55	78·11	76·48	55·23	54·62	57·33	56·51

TABLE 5.

Mean monthly evaporation, in cubic centimetres, and mean monthly saturation deficit, in millibars, at the Kikore Entomological Station, Tanganyika Territory.

Month	Mean monthly evaporation				Mean monthly saturation deficit	
	1928/29	1929/30	1930/31	1931/32	1930/31	1931/32
September	—	48	30	51	—	9·62
October	—	54	50	59	11·06	12·12
November	—	49	48	65	8·42	14·15
December	—	33	42	31	7·98	5·77
January	—	24	37	29	7·82	6·06
February	—	14	36	29	8·21	5·74
March	—	11	25	22	4·44	4·27
April	—	7	21	17	4·07	3·01
May	—	12	17	20	3·42	2·85
June	25	18	21	18	3·61	3·27
July	27	21	27	22	4·99	3·98
August	37	25	39	31	7·17	6·10

TABLE 6.

Rainfall, in inches, by months, at Kikore Entomological Station, Tanganyika Territory.

Month	1928/29	1929/30	1930/31	1931/32	Monthly means
September	0·00	0·16	1·66	0·08	0·48
October	2·25	0·94	0·27	0·00	0·87
November	0·47	0·31	4·23	0·76	1·44
December	3·76	6·88	1·25	9·16	5·26
January	1·70	7·66	5·83	3·73	4·73
February	0·50	6·95	4·13	5·81	4·35
March	5·38	9·75	6·85	12·62	8·65
April	5·90	13·33	7·84	11·23	9·58
May	0·65	5·09	2·50	4·75	3·25
June	0·03	0·06	0·12	0·06	0·07
July	0·05	0·25	0·00	0·03	0·08
August	0·11	0·01	0·00	0·00	0·03

(c) A study of some eco-climates of *G. morsitans* at Kikore and of physical factors as influencing the distribution of plant communities.

Two ecological investigations have been conducted in Kikore by the Tsetse Research Department. The first, a detailed study of the various conditions present, combined with organised observations on the fly, under Dr. J. F. V. Phillips, which was planned to throw light (*inter alia*) on (i) the action of the conditions on the plant communities and plant succession, (ii) their possible action on the puparia deposited in the soils, and (iii) the probable effect of the vegetational succession on the tsetse. The second was Nash's more frankly entomological investigation. The results of Phillips's investigation have not yet all been worked out, but a useful instalment has been published by J. D. Scott, formerly Research Botanist (Scott, 1934). The following is a brief abstract from his paper. Further particulars are given in appendix 4 to the present paper.

(i) *The methods adopted.*

Early in 1929 four ecological plots, each one-tenth of an acre in area, were laid out in each of six of the main plant communities at Kikore. Four plots, each one-fifth of an acre in extent, were laid out in each of the two main ecotonal (transitional) communities. It had been intended to include observations on the effect of game on the vegetation, but there was relatively so little game that observations at each station became practically confined to two plots at each, one of which was burned annually and the other protected throughout. Fig. 31 (on p. 462), representing the site shown on pl. 20 of Scott's paper, illustrates the effect in one of these plots of not burning the grass.

In each of the no. 2 plots, *i.e.* those burned annually and hence most like the surrounding vegetation, a very full set of instruments (listed by Scott 1934 : 188) was placed for the measurement of aerial factors—temperature, humidity at 6 inches and 4 feet from the ground, temperature at ground (grass minimum), solar radiation, sunshine incidence, light, and rain. In four of the unburned plots also, some instruments were placed at 6 inches above the ground for comparison with similarly placed instruments in the no. 2 plots. In each, quadrats and analysis circles were laid out for the charting of every plant at yearly intervals in pursuance of the study of succession; and in each a study of soil factors was initiated.

The latter included measurement of temperature, water content, water-supplying power of the soil, permeability, porosity, organic content, hydrogen-ion concentration (*p*H, soil acidity), maximum water-retaining capacity, hygroscopic coefficient, maximum shrinkage of soils, and colloid content.

(ii) *The types of vegetation studied.*

The types of vegetation studied were black "cotton-soil" mbuga, subject to three intensities of seasonal inundation, and a transition between these and the next to be mentioned, an ill-drained tree-Combretum enclave, an inter-zone between the last-named and the next community to be mentioned, a small wood of *Isoberlinia* and wooding of the mountain miombo (*Brachystegia microphylla*), the latter on nearly bare rock which prevented subsoil observation from being undertaken. Taken together, the results give an indication of the physical conditions which influence the distribution of the elements of the vegetational habitat of *G. morsitans*, as well as of the fly itself. Tables summarising some of the main results are in appendix 4.

(iii) *Conclusions.*

The following conclusions can be drawn from these tables :

(i) In the *Isoberlinia–Brachystegia* communities conditions are offered both to vegetation and to the tsetse, as regards insolation, temperature, shelter from strong wind, evaporation-rate and seasonal extremes of humidity and drought ("holard," or whole moisture-content of soil, seasonally 22 and 15%), which are far less severe than those which obtain in the mbugas of black alluvial clay; for these latter are open, inundated in the rains (holard 67%) and scorched and cracked in the drought (holard 2% only). They are less severe also than in the baked "cement" of the *Combretum Zeyheri* mbuga with its more open stand of small trees and its extremes of temperature—96·5° maximum, 39·5° minimum. *Acacia usambarensis* through its canopy, and less through its soil conditions, offers similar relief. Relative light intensity, lowest in the *Isoberlinia* (10% under canopy), was 13% in the *A. usambarensis* wood, 15% in the tree-Combretum and 30% under

gall-acacia. In the leafless seasons, the figures, in the same order, were 40, 40, 50, and 70. In *B. microphylla* it was rather high, 18–43%. In the spaces of the very open tree-Combretum it was 100% and would have been as much in those of the yet more open gall-acacias.

(ii) As regards the presence of well-drained soil, penetrable by the larvae, the order of suitability is obviously also from the *Isoberlinia–Brachystegia* (surface colloid percentage 12–24, resistance to permeation in *Isoberlinia* 4–6) to black mbuga (colloids 40–60%, resistance 16–20) and tree-Combretum mbuga (colloids 30–40%, resistance 40–60). *A. usambarensis* shows colloid 36%, resistance 24–35. "Resistance" has been taken by Scott as the time in minutes required for 1 litre of water to disappear into the soil, using the cylindrical steel tube method of Burger. The black alluvial soil in the long rains was "inundated;" *A. usambarensis* was "inundated for short periods;" the tree-Combretum mbuga with underlying "cement" was "very wet;" the *Isoberlinia globiflora* and *Brachystegia microphylla* wooding were "well drained." As hardness of soil prevents the larva from burying itself and extreme and continued wetness kills the pupa, the interest of these observations is obvious.

(iii) As regards probable visibility to the flies of the animals on which they feed, the order is reversed. Visibility is best in the black-soil mbugas during much of the year, though poor where the ground-cover of *Aspilia* is high, next best on the "cement" of the *Combretum* (still better on the cement of *G. swynnertoni* hard-pan areas), poorer in the *Isoberlinia* and *Brachystegia*, worse still in leafless thicket, and poorest in thicket in leaf.

It is interesting to note the general confirmatory effect of Scott's results on the explanations offered for the observed habits of the tsetse in relation to these various plant communities as described in the preceding sub-section (pp. 63 and 64 above). It is also interesting that the order of density of satisfied flies follows positively, and the proportion of females and young flies (seeking food) follows negatively, the physical transition from the conditions of the miombo at the one end to those of open mbuga at the other; and to notice that the conditions that Scott has proved to be harder are faced only by the hungry individuals, while those which are satisfied stay comfortably in the shadier woodlands, which also provide the main breeding-grounds. This, with one recorded exception (noted on p. 83 below), refers even to males in search of females.

TABLE 7.

Rainfall, in inches, from three stations half a mile apart at Kikore, Tanganyika Territory, showing variations within short distances.

1929–30	Station B	Station E	Station G
July	0	0	0
August	0	0	0
September	0	0	0
October	0·65	0·59	1·28
November	0·62	0·45	0·90
December	6·76	6·15	6·31
January	7·31	7·07	5·31
February	7·89	6·23	6·55
March	13·82	8·75	11·21
April	11·57	11·57	11·93
May	4·73	3·68	4·18
June	0·14	0·11	0·07
Total	53·49	44·60	47·74

(d) Probable small changes in eco-climates from one year to another.

Rainfall has a profound effect on the date and incidence of leaf-fall and on the herbaceous vegetation. The table on p. 68, quoted from Scott, is interesting as showing how much the rainfall may vary within very short distances and indicating that from one year to another the eco-climates of a particular spot may not be the same.

(e) The round of the seasons and its effects on adults of *G. morsitans*.

(i) *The round of the seasons.*

In the greater part of the Tanganyika Territory there is some trace of the short dry season in February. It is very marked in the north. Where it occurs the course of the seasons is roughly as follows, though annual variations occur.

The early long dry season extends from May to July inclusive. The rains cease early in May. For a time conditions are probably specially favourable to the flies, much shade still remaining and the air and the ground losing the extremes of humidity which characterise them during the rains.

The grass dries and in many localities leaf-fall is already marked in June, being hastened by the advent of cold weather. In exceptional localities, like Kikore, where the sky remains overcast daily till as late as 3 p.m. in much of the dry season, leaf-fall is slow to begin. In 1934 yellowing here and there was beginning in July, at a time when, at Itundwe, 30 miles farther south, much fall had taken place and in other parts of the country (as Singida) the fall was nearly complete.

In June the weather turns cold, and in July in Kikore the minimum temperatures occur. The grass dries out rapidly, and in July the grass fires, lighted by the natives, have begun. By August the country becomes fairly burned out, although, owing to the poorness of the grass in many miombo areas and to the unorganised nature of the burning, patches of grass remain everywhere. But the annual grass fire is for the woody vegetation and all that inhabits it the great event of the year. Plants of the rain forest and allied communities are prevented from establishing themselves at all. Even of the savanna species the young shoots from underground roots are nearly everywhere burned back and the bush is prevented from densifying. The trees are rendered leafless, in so far as the normal leaf-fall has not produced this effect already. The sandy soil is bared to view and to the heating effect of the sun, and the blackened bases of the grass tussocks that have been burned dot it over. Much even of the leaf-litter has been burned. A period of intense desiccation is ushered in. This is the late dry season, August to October.

The cold spell has passed, and the temperature rises until the end of the long dry season in November, shortly after the sun has reached its zenith. Before the rains the heat is intense. As the trees are leafless, the rays reach most of the ground. Saturation deficit increases progressively till the rains. Evaporation readings by means of the Livingston atmometer, even in Kikore, where the season is a month later and certainly less intensive than in the larger fly belts in Tanganyika, show the highest evaporation as taking place at the end of the long dry season. Sunshine and light intensity maxima occur.

The one bright feature from the point of view of animal life is afforded by the margins of mbugas—of the drainage valleys and glades. In many, but not all, of these margins, leaflessness is of short duration. The leaves last up to the fires better than elsewhere, and very soon afterwards the strips of *Combre-*

tum ternifolium which line the mbugas are putting out dense tender leaf. The miombo trees just behind them follow suit. Even in 1934, a season which followed deficient rains, the edges of many of the mbugas of the great western (Tabora) *morsitans* belt were already shady in September. In the first days of October the green flush had in places begun to extend up the lower slopes and odd trees showed pink or green even in the miombo of the hills. In parts of certain of the mbugas the grass also comes out green soon after the fires and, if water is available, the game animals tend to congregate there out of all the surrounding miombo, where the conditions are still those of a furnace. The cicadas are everywhere calling, but visible insect life is at its annual minimum.

(α) *First (short) rainy season (November to January).*

The first thunder showers at once bring about a general flushing both of the trees and of the grass. Humidity returns to the air, insects everywhere appear, and the game animals scatter as water-pools and grass become better distributed. The whole country becomes transformed. The temperatures somewhat decrease. High temperature returns between showers, but mitigation can always be obtained by insects and vertebrates if desired through the abundance of shade. The scattered, young, green grasstufts are short; there is still plenty of bare ground between, such as the tsetses love to settle on, and visibility remains excellent.

(β) *Short dry season (February).*

The second sunshine maximum of the year occurs. Very high temperature—also the second maximum of the year—is experienced, and as a rule, a drop in humidity and a rise in evaporation which are remarkable considering the shortness of the period. The leaves of the thickets wilt. Sometimes some of the grass burns again. But abundant shade is available everywhere. This period is probably even more favourable to the tsetse than are the short rains. In some years (*e.g.* 1930) after much rain has fallen in the first (short) rainy season, the rise of temperature in February may be small.

(γ) *Second (long) rainy season.*

Heavy shade, sustained humidity (the maximum for the year), and long grass (though the grass of most miombo wooding does not grow long). Nevertheless, the ground is covered and is kept constantly moist. Food animals are still well-distributed. The temperatures decrease until the minimum is again reached in July.

TABLE 8.

Rainfall, in inches, at the Kikore Entomological and Ecological Stations, one mile apart, in Tanganyika Territory.

Season	Kikore Entomological Station 1928/29	Kikore Ecological Station	
		1929/30	1930/31
Long dry season, June to October . .	2·66 *	—	1·62
First rainy season, November, December, and January	5·93	14·69	14·18
Short dry season, February	0·50	7·89	2·38
Second rainy season (late February), March–May	11·93	30·12	16·04

* The figure for the month of June 1928 is not available. June 1929 has been taken.

(δ) *The rainfall of the four seasons.*

The table on p. 70 brings out clearly the difference in the seasons as regards rain and the fact that the first rainy season is sometimes deficient.

(ii) *The effect on the hunger of the flies.*

Jackson's method of hunger-staging, as stated already, has proved most informative in the hands of all members of the Tsetse Research Department in Tanganyika. Regularly, as the evaporation rate has risen, the hunger of the flies has increased. The late dry season is a period of intense hunger, when the hunger-cycle, *i.e.* the period between feeds, becomes four days only, or less, as compared with eleven or more in the rains.

(iii) *The effect on the density of the flies.*

The best record in Tanganyika of the effect of the physical factors on the density of the flies is supplied by Nash's fine work at Kikore, continued without interruption for more than four years. The following is taken from his paper (1933*a* : 118).

(α) *The effect of cold.*

Dry years are characterised by the severity of the cold spell that occurs in June, July or August. The mornings are bright and crisp, and near dawn it becomes very cold. In early August 1929 the mean minimum screen temperature in an " mbuga " from 9th to 14th August was 41° F., the lowest reading being 39·25° F.

The high fly densities found at the end of the heavy rains continue only until the advent of the cold spell, which may (as in 1928) come as early as June or (as in 1929) not till August. At the close of the cold spell the fly density rises transiently, prior to the invariable late dry-season fall. In 1929 there was a long period of high fly density in May, June and July, accompanying higher temperatures. The cold was so late this year that the fires followed almost immediately, preventing any recovery after it.

The freshly emerged fly numbers remain up, despite the drop in total fly density. This is an important point, as it suggests that the cold affects the total density through killing off the old flies, leaving the freshly emerged individuals unharmed. If anything, the cold stimulates emergence.

(β) *The effect of variation in the evaporation rate.*

Nash compared the seasonal variations in the evaporative power of the air, as measured with Livingston atmometers, with the variations in fly density as indicated through the years by his north-east Kikore round, which is not affected by game movements.

His graph, reproduced here as fig. 9, shows the seasonal variations in fly density and evaporation and is the subject of his remarks as follows :—

> " Let it be assumed that a mean monthly evaporation of from 20 to 25 ccs. a day affords an optimum condition for fly. It will be seen that as the evaporation increased above the figure, so the fly density decreased. At the end of the dry season, October 1929, the evaporation reached its maximum of an average of 60 ccs. a day. Hence this month may be considered to have afforded the worst conditions for the fly community. By the next month the fly density had reached a minimum. The early rains now broke, the evaporation fell with the moister atmospheric conditions, and fly density started to rise in the following month (December). By

January 1930 the evaporation had dropped to within the alleged optimum zone of 20–25 ccs. a day. Yet again, after a month's lag, the fly density reached its second maximum point. So far the correlation has been negative, as one goes up the other goes down. But drops in the evaporation below the optimum zone are also succeeded by a drop in fly density."

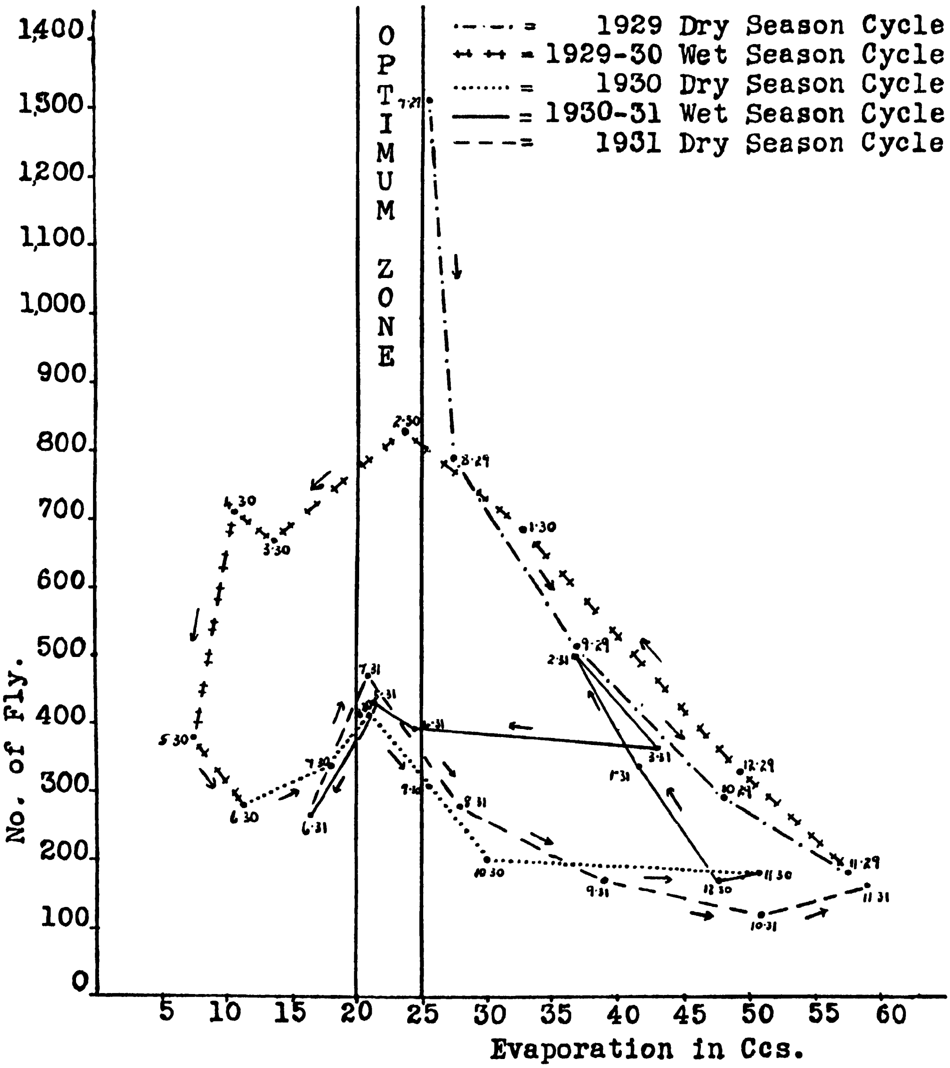


FIG. 9.—Density of *G. morsitans* at Kikore, as deduced from the fly-round captures, plotted against the evaporation of the previous month from Nash, 1933 : 125. Months (11·31 = Nov. 1931) refer to the month when the flies were caught; not the month of the evaporation. The points have been joined in monthly order. Each annual cycle falls into a dry-season and a wet-season cycle.

Lack of space prevents further description here of the courses followed by the two curves, but it will be seen from the graph in fig. 9 and from the account of the seasonal fluctuations below that the reactions of the flies

continued to be similar to those described above. Any small deviations are explained by Nash by the observed intrusion of other factors, as a concentration of game on the fly round. " The lag . . . when taken as a month gives good results on the graphs " (Nash).

(γ) *The evaporation through the seasons.*

Nash correlates as follows the seasonal changes in the evaporative power of the air with the variations in his fly counts over his four years of observation as follows :—

(δ) *Late dry season (September and October).*

In this period the evaporation rises and fly density steadily falls to its minimal point for the year. It is true that at this time certain limited areas increase in their local fly density owing to a concentration of flies within them, but the population has generally fallen greatly. It is characteristic of large areas in Portuguese East Africa and Rhodesia that considerable pieces of country are at this time evacuated or practically evacuated by the fly in favour of far-separated concentration grounds.

(ε) *Early rains (November to January inclusive).*

Density remains throughout November at the same minimal point that it reached in October and this minimal figure is approximately the same each year, no matter whether the fly was abundant or scarce earlier in the year. Throughout December and January (during the early rains) density steadily rises, owing to the fall in the evaporation.

(ζ) *Short dry season (February).*

Fly density reaches a maximum point during this month every year.

(η) *Heavy rains (March and April).*

Fly density falls slightly, owing to the temporary rise in evaporation during February. Density then remains at a steady medium high level each year, lower than that of February.

(θ) *Early dry season (May to August inclusive).*

(1) After poor rains. A great increase in fly density takes place in May at the end of the rains, a maximum being reached in June. In 1929, when the rains were very poor and there was famine in some districts, this increase in fly numbers was very marked. Nash wrote :—" About July the cold spell causes a drop in fly numbers. Fly density recovers at the end of the cold spell, but before long starts to fall towards the late dry-season minimal point. (2) After very heavy rains, and a very wet April. In early May the fly density is steadily falling. It reaches a minimum point in late May or June. As the country dries up the density rises, reaching a relatively high figure in August, after which it starts to drop towards the late dry-season minimal point."

(ι) *Summary regarding seasonal fly density and the effect of evaporation.*

One can say that for three-quarters of the year, namely from August until April inclusive, the seasonal fluctuations in fly density occur every year, without fail. May, June and July are the months that compose the inconstant quarter of the year. The fluctuations in fly density for this period, which follows the heavy rains, depend upon the rainfall preceding.

The late dry season is the most constant of all seasons. Every year the bush fires burn up the country-side, the trees become leafless, and the maximal temperature is attained. Nash believes that the constancy of this season, and the relatively small variations in meteorological conditions therein from year to year, account for the small variation in fly numbers from one December to another.

His explanation of the effect of the evaporation is that it affects the longevity of the fly. Jackson's work suggests that the reduction of longevity is due largely to deaths from hunger. The effect of cold on *old* flies, suggested by Nash, may prove to be a real effect also, but needs to be tested in the laboratory.

The evaporation rate, as ascertained by means of an atmometer, gives an integration of the effect of temperature, humidity, wind, and barometric pressure, and has proved a most useful measure of the combined effect of the factors most affecting the flies.

(f) The effect of season on the breeding of *G. morsitans*.

Emergence of young fly from their puparia is least at the end of the long dry season and beginning of the early rains (October and November) (Nash). It decreases as the dry-season conditions become more severe until it is almost at a standstill—perhaps partly due to falling density of the parents. " Emergence is greatest at the end of the early rains and throughout the short dry season (January and February)." There is a great burst in late January and February. " Throughout the heavy rains but little emergence takes place (March and April). In dry years there is much emergence at the end of the heavy rains (May to July), but this does not occur after very wet years. . . . Generalising, one can say that breeding is greatest when the evaporation curve approaches the vicinity of the optimum zone " (Nash).

It should be added, however, that there are places in which a great burst of emergence takes place with the warming up of the weather after the cold spell, presumably from puparia produced during the early dry season. Moreover, Jackson's and Potts's field observations, from other localities, which are based not on the young flies but on the puparia themselves, are not in conformity with Nash's. Further, in the laboratory Potts found (as did Buxton and Lewis in Nigeria) that the tendency to larviposition was strongest under conditions of drought.

Jackson found *morsitans* puparia " comparatively very abundant at Kakoma and all over Tabora in October, whereas at the close of the long rains hardly one could be got. . . . Thus laboratory work and at least some field work indicates that larviposition is by no means greatest with evaporation in the optimum zone—and we must remember that the numbers of pupae continue fairly high when, as we suppose, adult flies are decreasing, from, say, August to October " (Jackson, *in litt.*).

In the case of a very large number of *morsitans* puparia collected by myself in Portuguese East Africa, I found that larviposition was going on both in June and July and in some quite cold weather, but that emergences from the pupae secured only began to take place in numbers with the advent of really warm but dry weather in early September and continued into November (Swynnerton, 1921 : 365). It is certainly likely that the specially large numbers of puparia to be found in some localities towards the end of the dry season represent in part the larviposition of, say, two months previous.

(g) The effect on *G. morsitans* of varying types of rainfall.

(i) *The effect of a deluge on a low-lying fly belt.*

Throughout 1929 and early 1930, Nash records that the fly community at Kikore was positively thriving. For the rest of the year, and for the whole of 1931, the tsetse population was clearly struggling against some severe calamity that had overtaken it in April and May 1930. It is not until early 1932 that the fly can be said to have recovered. There can be no doubt as to the nature of the blow. It was in April and May 1930 that the torrential rains of that year reached their climax. Towards the end of April ten inches of rain fell in eight days, an amount equal to half the total rainfall of the previous year. The investigators went splashing through quite deep water on parts of their fly rounds and fish swam in the grass-lands.

The effect of the torrential rains was even greater on the Kandaga round than that of south-east Kikore. The escarpment behind the Kandaga round is mostly unsuited to breeding because it supports 14-foot grass, so that these hills were unable to form a refuge from which re-infestation might occur. The result was that Kandaga almost ceased to be a fly belt. In early June the twelve miles of this round could only yield 22 flies [or 10·4 per 10,000 yards] of which 18 were freshly emerged. Kandaga is of great practical interest as a natural example of the extent to which fly density can be reduced without extermination resulting. The flies may have been affected in one or more of four ways :—

(1) By the extermination of the old flies owing to the unsuitable meteorological conditions. For seven consecutive days in late April the atmosphere was saturated, no evaporation taking place.

(2) By arrested reproduction. Roubaud (1909) found that *G. palpalis* reproduces normally at 70% relative humidity, but that a humidity of 100% arrests reproduction.

(3) By the incidence of an entomophagous fungus that produced black spots on the lower side of the abdomen of the tsetse and, under the trying conditions prevailing, apparently killed it. The fungus is in the Phycomycete group, and Potts has found it to be non-lethal under ordinary conditions.

(4) By part of the plains being inundated for some weeks, and most of the bush water-logged. It seemed highly probable that submergence of tsetse puparia might prove fatal (Nash, 1933*a*).

Experiments by Nash duly showed that immersion for more than four days was fatal. He considers that the entomophagous fungus did not play the greatest part in the reduction of the flies. If the fungus had been of primary importance, the north-east Kikore round should have suffered equal reduction. He concludes " that the effect upon the fly community was primarily brought about by the destruction of puparia, owing to the inundation and water-logging of the breeding-sites, and secondarily by the cessation of larviposition due to arrested reproduction. . . . " But the old flies also disappeared.

(ii) *The effect of a deluge on a well-drained fly belt.*

As regards Kikore, where these observations were made, the fact must not be overlooked that a large proportion of this exceptionally narrow fly belt is low-lying and is readily flooded by such downpours as closed the rains of 1930. The tsetse was stated to have been similarly affected in the neighbouring fly belt of Babati, a large proportion of which also is easily flooded,

and in the long-grassed, heavy-rainfall area of western Handeni. The *Acacia pallens* areas at Kilosa will certainly have been drowned-out like Kikore. On the other hand Potts and Jackson visited the *morsitans* belt of Sambala (which is far more typical as regards the proportion of drained and undrained ground, and which, being in the same district as Kikore, shared the deluge) in the dry season following the latter while the fly numbers at Kikore were still at a very low ebb. They repeated one of our old rounds and found the fly numbers very greatly increased. Further, this was the year in which a particularly strong advance forward took place on the part of the western Kondoa belt in which Sambala is situated. Nash himself states in addition that "the well-drained north-east Kikore fly round was not nearly so badly affected as the other two rounds."

One is inclined to conclude that a deluge which may destroy a fly community on alluvium either may affect it only slightly or may stimulate its population to increase under well-drained conditions.

(iii) *The effect of abnormally heavy rains well distributed.*

Nash has shown that it is quite possible to have an abnormally heavy total rainfall figure and yet a quite unaffected fly community. "During the biological year 1929–30, when the fly were so nearly exterminated in May 1930, the total was 51 inches, whereas in 1931–32 the total was 48 inches; yet in this latter year the fly, though conforming to the wet April type of fluctuation, were in no danger of destruction at the end of the rains. Though the total rainfall figures are so similar, yet in 1929–30 the rainfall was badly distributed, there being an aggregation of wet days in April and May, whereas in 1931–32 the precipitation was well distributed" (Nash).

(iv) *The effect of defective rains.*

A poor rainy season at Kikore, the peculiarities of which station must, however, be borne in mind, is particularly favourable to *G. morsitans*, the numbers of which soar in consequence. For this Nash's graph (*see* fig. 9 on p. 72) should be consulted. When I myself repeated the fly rounds at Kikore in 1934 after two poor rainy seasons, I found fly numbers high again. Such a season as 1934 in the Tabora belt might, on the other hand, result in much destruction of flies and an exceptionally reduced concentration of the survivors in a few places only.

(h) The effect on the feeding-grounds.

"During the drier times of year the tsetse become hungry [or thirsty] at short intervals. At such time a high proportion of the total population is found waiting for food in the 'restaurants,' and as these flies are hungry they are correspondingly more evident to the casual observer. In the damp months tsetse flies become hungry relatively very slowly, and many individuals (therefore) are able to satisfy their hunger by chance meetings with animals passing through the 'home.' The home at such times thus takes on the character of a hotel, and the restaurants are found to be comparatively little used by flies seeking for food" (Jackson).

(i) The effect of season in causing contraction or shifting on the part of *G. morsitans*.

(i) *The history of the observations.*

It has long been known (Jack, Shircore, Johnson & Ll. Lloyd, Swynnerton) that *G. morsitans* evacuated in the late dry season considerable areas

of wooding which in the rest of the year it had occupied but which now had become inhospitable, and concentrated instead at certain of the drainage basins and glades and, in Nigeria, in the riverine thickets. Jack referred to this in 1911 and drew strong attention to it for Southern Rhodesia in 1912 (*Bull. ent. Res.*, **2** : 360). " It has already been stated that *G. morsitans* congregates on the shady banks of the rivers and borders of vleis in the dry weather. In the wet season, when the forest is shady, the fly is much more generally distributed through the veld " (Jack, 1912). Shircore in 1914 (*Bull. ent. Res.*, **5** : 89–90) recorded the same observation for Nyasaland, described how the flies, spreading with the rains from their " primary foci," occupied temporarily " secondary foci," which now were becoming equally suitable, and he suggested the concentration of attack at the foci. I extended this observation to Portuguese East Africa (Swynnerton, 1921) and Lloyd & Johnson to Nigeria. The investigation of the reason for such concentrations was amongst the points laid down by myself at the start of the work of our team and led to the discovery of the feeding-grounds.

(ii) *The position in different types of fly belt.*

(α) *Miombo* morsitans *belts characterised by feeding-grounds only.*

Feeding-grounds only, or chiefly, without additional seasonal evacuation of large areas of the miombo, were found to characterise the Kikore and Sambala fly areas, so much so that Nash regarded the miombo in Kikore as his dry-season concentrating-ground. Here concentration, other than that which takes place all the year round at the feeding-grounds, is not marked.

(β) *Large miombo areas in which seasonal contraction takes place.*

In Portuguese Territory I found that the flies concentrated seasonally and bred (to a moderate depth) in the miombo bush bordering certain " vleis " or " mbugas," which were doubtless the feeding-grounds, when the great areas of similar miombo country between, in which vleis without dry-season shade occurred, were to all appearances being deserted. This appears also to be the common position in Southern Rhodesia. The miombo belt at Kikore is so narrow, that it is only equivalent to the infested miombo strip which margined the mbugas that I observed. In any case, with its protracted dry-season cloudiness and consequently long-retained leaf, the Kikore miombo generally offers specially favourable dry-season conditions to the flies. In Sambala, the feeding-grounds having favourable contacts with the other bush-types required by the flies were sufficiently close together to avoid very noticeable evacuation of country between. In areas which contain wider stretches of uninterrupted miombo it is very different, as Jackson found when investigating the Tabora belt in 1934.

(γ) *Miombo belts in which concentration is present throughout the year, the rest of the belt being permanently sparsely infested.*

In an area of 1,500 square miles which was studied in South Tabora, the flies were collected in the late dry season of 1934 (following defective rains) into concentrated aggregations which occupied particular portions of three patches of country which together amounted to a small proportion of the whole and formed the general dry-season habitat. A piece of fairly open land, with low *Dalbergia* wooding but with large trees and denser thickets on the ant-heaps, a reach of a dry stream with thickets at frequent intervals along it and water-holes which last late into the season, and gall-acacia " mbuga " with

miombo round it which flushes early, are typical of the vegetational sites of these concentrations. In every case a varied interspersion of vegetational types is present. Miombo wooding is in each instance close by, to play its own part and also to afford communication with the great evacuated areas of miombo that may be again infested later on; in every case mbuga, open in parts at least, is alongside; and in each site there is good shady cover which is being used for breeding, whether the miombo itself supplies it or whether it has to be sought in thickets on ant heaps and streams. In each case the concentration is at a concurrence of vegetational types, forming the " edge " or " contact " effect which we have long learned to associate with such aggregations. In each case game is present in some numbers and is a factor to be reckoned with, but it is not in numbers greater than, or as great as, may be found in uninfested country close by.

The lack in the vegetational concurrence of an element providing good shade (the " massive wooding " element of *G. palpalis*) might account sufficiently for the evacuation of the general *Isoberlinia–Brachystegia* in south Tabora in the season of stress, as happened in Portuguese East Africa, for game persists at some of the very numerous temporarily shadeless and flyless contacts. Even in the rains, however, to the date of writing, there has been little dispersal, and the intervening country remains, and promises to remain, a fly-sparse area. There are also other sites which, both as regards game and concurrence of the right vegetational conditions, appear to be as fitted to be concentration sites as those just referred to, which are, however, unoccupied by the flies. It may be that some factor is missing. It may, on the other hand, be that the fly population is too small to occupy all the optimum sites, but that if one site were rendered unsuitable another might come into use, as appeared also to be happening in Mossurise (Swynnerton, 1921). It may prove (*a*) that over a great deal of the country apparently suitable but not occupied permanently or fully there is insecurity of tenure through undependable game-habits and densities; (*b*) that this has contributed to the probability that there is an insufficient fly population to fill all suitable sites economically; and (*c*) that the sites actually filled are filled economically, *i.e.* that the density of the flies shows a tendency to approach the optimum for the purpose of survival and reproduction, and that avoidance of such crowding as will invite over-destruction by enemies, desertion by food animals and over-interference with breeding by the male tsetses, if such should take place, is being assured sufficiently by these factors themselves, while such scarcity as might hinder the meeting of the sexes has been avoided by concentration. This question of the social habits of the flies is under preliminary investigation.

Here (*see* Elton, 1933, and the definition given in appendix 1) the economic density for the fly in the dry season is undoubtedly that found in the patches of country which include the concentrations. In relation to man, however, the " lowest density " is also the " economic " density, for it is the wide distribution, though low density, of the fly over stretches of country in the rainy season and otherwise which determines where cattle can be kept. In addition, the " highest density " reaches its highest point when the " lowest density " (whole population) of the insect is near its annual minimum.

In the concentration sites in south Tabora, the flies generally are not hungry, except on the margins of the mbuga. The individual concentrations are thus once again divisible into home and feeding-ground. The scarcity in Mossurise of the right vegetational " contacts " in the dry season, as opposed to their greater abundance in the rains and in Tabora perhaps a scarcity all the

year round, as opposed to an abundance of them in Sambala all the year round, affords an excellent illustration of Leopold's "law of interspersion," which runs: "the potential density of game [in this case "fly"] of low radius requiring two or more types is, within ordinary limits, proportional to the sum of the type peripheries."* However, in cases that alter seasonally, it seems clear that, despite the ubiquity of favourable combinations in the rains, the reduction imposed on the fly population in the dry season must affect its occupation of them during the rest of the year.

In any case, lack of a sufficient shade element adjacent to the more open requirements of the fly is probably often in its drier habitats the immediate motive of seasonal concentration, though the survival effect of concentration, holding together as it does the sexes of a reduced population, must be an important motive in all cases, seasonal or permanent.

(δ) *Bush types other than miombo.*

A tree-Combretum enclave was noted as evacuated in the late dry season at Kikore and broken thickets were then being used by the fly. Burtt's investigation of the Itigi thickets showed that, for some distance in, these also were used at that time of year (see pp. 310 and 315 below). These are therefore, instances of the opposite process, namely, the extension of range in the dry season.

5.—THE EFFECT ON *G. MORSITANS* OF GRASS FIRES.

(a) The effect of the ordinary annual grass fires.

(fig. 8.)

Though grass fires are in origin biotic, their effect on the fly is to increase suddenly and greatly the severity of the action of the physical factors. They usher in the critical season of the year.

Of this, Nash writes :—

> "If a fly round is done the day before the fires, and then again on the day after the fires, the total catches for each round will be about the same. However, the distribution of the fly will be found to have changed entirely. Areas that formerly supported thick fly and have since been cleanly burnt will be found evacuated and islands of bush that escaped the fire will yield abnormally heavy densities. . . . *G. morsitans* has been watched flying ahead of a poor fire that was creeping through *Isoberlinia* wooding towards the road. The fly seemed quite unperturbed, but were abnormally dense. . . . If density was not already decreasing at the time of the burn it will decrease some time afterwards. It is believed that [the ordinary] fires merely accelerate and accentuate the features of the late dry season. The gradual process of leaf-fall in the open savanna and the temporary evacuation of this country by fly are accelerated by the fires, and the rising temperature and evaporation are accentuated by the burn. The adverse effects of low humidity and heat are greatly heightened by the burning of the grass and the complete defoliation of the trees. The radiation from the black ash-strewn ground becomes intense, and the fly density decreases rapidly owing to the supposedly reduced longevity of fly under such extreme climatic conditions."

* See also pl. 6.

(b) The effect of organised fires late in the season.

(pl. 14, fig. 2.)

The effect of organised fires late in the season must be clearly distinguished from that of the ordinary annual grass fires discussed above. Early unorganised fires are seldom extensive and later unorganised fires merely drive the flies into the sites burned before, from which they quickly spread back. Our organised fires have for their object a purposeful drive of the flies across a barrier over which they will not return. While no purposeful attempt has yet been made to drive *G. morsitans* out of a piece of country by means of late, organised grass-burning, the indications from experimental fires are that this fly reacts similarly to *G. swynnertoni*. Much of its country is too lightly grassed for this measure, but where the grass is suitable, it is usually not characterised by the hard-pan strips which in *swynnertoni* country assist the flies to cling on.

6.—THE SUCCESSION IN THE MIOMBO AND THE EFFECT ON *G. MORSITANS* OF CEASING TO BURN THE GRASS AND OF SO PROMOTING THE ADVANCEMENT OF THE VEGETATIONAL SUCCESSION.

(pl. 11.)

This is one of those measures by the use of which very small effort and slight expenditure may transform the whole face of an appropriate piece of country to the disadvantage of a pest—and which, in our experimental area, appears to be beginning to do so by substituting for interspersal of vegetational types one only of the types of country needed by the flies. It is therefore proposed to devote some space to a discussion of the vegetational succession, first here under *G. morsitans*, and later under *G. swynnertoni* (pp. 87–89 and p. 100), and "thicket-barriers" (p. 307). For the manipulation by us of this succession appears at present to be the most feasible way of dealing with the tsetses referred to. Our actual experiments and their results up to the present are described for *G. morsitans* on pp. 275–278 below, and for *G. swynnertoni* on pp. 272–274 below.

(a) The general position.

Only in comparatively limited areas in tropical Africa is it likely that the ecologist's ideal and orderly sequence of succession from the bare rock, through herbage of increasing wealth, to shrubs and thence trees of ever-growing luxuriance, will have been followed in the last few hundred thousand years. Several indications suggest that it is likely that the country has been covered fairly generally through a long geological period with woody growth of close density and of a luxuriance varying in time and place from that of tropical rain forest to that of deciduous thicket. With the introduction on a large scale of the cultivating and grass-burning activities of man there have spread also the fire-swept but fire-surviving savannas which, wooded and less wooded, have supplanted in great measure the dense forest and dense thicket types as these were driven from the land. The soils have probably grown progressively poorer rather than richer where large human populations have been present, for the efforts on the part of the vegetation to recover lost ground, which ecologists name succession, have continually been "headed off." We are still in this age of destruction. Our instruments are the annual fires which sweep nearly the whole country each year (for some of the evidence of their results, *see* Swynnerton, 1917) and the removal of the soil by wrong methods of cultivation and by suicidally intensive overgrazing.

(b) The miombo as a sub-climax.

When the day for recovery comes, miombo does not wait for the grass and shrub stages to pass. It has a great facility for growing even on bare shale or broken rock surfaces and, if only its seeds be provided, is apt to be in at the start.

Once in full possession of the ground, the greedy miombo tends to keep this bare of the grasses and clear of possible competitors unless the soil and the rainfall are sufficiently good to enable all to subsist. Even then, while the grass may be good, the annual fires will help the miombo to keep the ground clear of any general shrub up-growth and therefore to provide conditions suitable for *G. morsitans.* This may be seen happening to-day over great areas of Africa.

The succession back to density stands arrested and, so long as the fires go on, miombo and *G. morsitans* will remain as the vegetational and tsetse sub-climax, in this case "fire-climax," beyond which succession cannot go. What will happen if we keep out the fires?

(c) The effect of excluding grass fires.

In one type of miombo country, with the fires kept out, the miombo will still be strong in its intolerance of any competition, and the ground will remain so clear of competitors, even of grass, that, at least for a long time to come, little change will occur. This condition, after a few years of non-burning, is visible to-day in a part of Singida and some of the Kazikazi country. The miombo has thoroughly entrenched itself.

In a second type, which covers great areas, the grass growth at least is sufficient to add annual humus to the soil, if it be not burned off, and so to increase the prospect of there being later enough food there for more than the miombo alone. Further, over appreciable parts of these areas, there exist the live roots of saplings and shrubs, burned off hitherto, which spring up and sooner or later form thicket, in which at the moister end of the miombo's range savanna-tree seedlings will not thrive, though thicket seedlings will do so. Where this latter happens, as it has in our experiments at Kikore, the thicket ultimately resulting should at long last be instrumental in expelling the miombo and inaugurating the continuance of the succession on orthodox lines, to the disadvantage of the tsetse. In rather drier conditions miombo may persist as a canopy over the thicket, broken or closed, composed of its own saplings and various shrubs—still to the disadvantage of *G. morsitans.* This at present seems to be the position at Itundwe.

In a third type a seed-supply of appropriate thicket or of rain forest is at hand. What is appropriate thicket? In other words, what successfully invades unfired miombo? It is important to know this for the areas which will not densify automatically.

At the damp end of its range miombo has actually been seen to be invaded—and on nearly bare shale—by rain-forest elements adjoining it when the grass fires were stopped. Quite ordinary *Isoberlinia, Uapaca,* and *Brachystegia* were thus assailed, the great rain-forest lianas throwing their arms out over them in a smothering embrace, and the bird-sown elements of rain forest and of its outskirts coming up thickly below them. Further from the seed supply of the rain forest, deciduous thicket was the first invader. The rainfall was high, averaging 60 inches.*

* "The pyrophobe trees . . . *Ekebergia Meyeri, Pygeum africanum, Teclea swynnertonii, Sapium Mannianum* and *Sizygium guineense,* but especially, and in numbers, the

At the dry end of its rainfall scale (perhaps 23 inches) miombo which had suppressed the grass has been locally invaded by so drought-standing a deciduous-thicket element as *Abrus Schimperi*, though possibly on mixed-soil conditions. Elsewhere other shrubs normally confined to the ant heaps have been seen to spread thence through the wooding.

Rain forest and *Abrus* thicket are connected up by a series of distinctive dense forest and thicket types which range from evergreen to seasonally leafless, from high rainfall supporters to low. Actual observations suggest that miombo, with its wide rainfall range, might be directly invaded by several of these, given the rainfall or soil conditions that will enable the invaders to compete.

A thicket type which will not invade miombo, except where the residues of its own " duricrust " soil are present in the miombo granite, and that miombo cannot have antedated on the thicket's own ground, is the " Itigi " thicket (*Burttia–Baphia*) described on p. 307 below.

(d) The nature of the climax.

The climax reached will certainly not be a single one; even the dense wooding types which may replace the miombo will differ in their components and character, and there may in addition be climaxes of the *Isoberlinia–Brachystegia* itself, (i) with denser undergrowth, (ii) with little—each to be seen already in particular unburned localities. Nor is each variety of climax at all certain to represent what stood on the ground originally, for conditions will have been so changed and so much extermination of thicket species will have taken place that " deflection " will certainly occur. The ultimate end of each road is likely to be discovered if the inexpensive experiments which we are initiating to-day in connection with the tsetse are kept up for an indefinite period.

(e) The effect on *G. morsitans*.

It would seem from much observation that any considerable return over a large piece of country towards a rain forest or dense thicket climax must mean the disappearance of *G. morsitans* and, if we allow it, its replacement again by its probable predecessors—the tsetses of the denser conditions. To prevent this last, while encouraging the first, is our problem in those places where we use the succession. The other fear is that the change may take so long to come about that the cost of the measure will, in the end, be excessive. There are large stretches of country to which this fear does not seem to apply.

Non-burning experiments against *G. morsitans* are being continued at Kikore and Itundwe and, with the changes in the vegetation and the fauna which they should, gradually, bring about, will form an important and closely watched item in Jackson's forthcoming work against *G. morsitans* at Kakoma, south of Tabora.

7.—THE MATING ORGANISATION OF *G. MORSITANS*.

The males of *G. morsitans* which are not so hungry as to be searching for food may be found chiefly " loitering "—as standing catches have shown—

pioneers *Haronga*, *Albizzia*, and, to a less extent, *Bersama*—are entering into successful warfare with the pyrophytes of the lower slopes, while the big climbers *Landolphia*, *Choristylis*, *Canthium*, *Rhoicissus*, *Uvaria*, *Secamone*, and *Lygodium subalatum* are flinging themselves out over Brachystegias and Uapacas and already smothering some of them. That the pyrophobes should be capable of growing up under trees so exclusive and hard on the ground as the last two genera has interested me immensely " (Swynnerton, 1917).

in the rest-haunt, which contains the main breeding-grounds, and in the inter-zone between this and the feeding-grounds. Here two of their habits, at least, help them to make contact with the females. One is that of collecting on paths and other patches of open ground, which are visited also by females; the other, assisted by this frequenting of paths, is the habit of forming a "following swarm," whether merely of two or three or of a hundred or more individuals on man or other animals passing through. In their inclusion of man for this purpose they differ from the males of *G. palpalis.*

The males of the following swarm are there for one purpose only—the interception of females coming to feed. Their behaviour varies much with the day. They may actually settle on men or animals and fly off thence to accost flies which they detect in the air, or they may follow along by short flights, settling each time on the path ahead or behind or on bare ground between the tussocks of grass on either side of the walker. It is probable that from the ground other flies, which may be females, are detected against the sky, and in any case it is certain, both from captures and especially from observations of Jackson's in relation to traps, that females "follow" in like manner, though more surreptitiously, and hungry females in any case come boldly to feed.

In an instance seen by myself in Portuguese East Africa definite swarms of males, small or of moderate size, which I then called "male clusters" (Swynnerton, 1921), used to frequent the margins of open feeding-grounds, evidently, from what was seen to happen, with the purpose of finding females.

8.—THE DISPERSAL OF *G. MORSITANS.*

The statements under Part 4, Section B (pp. 297–300), except when otherwise stated, apply to *G. morsitans.* The subject is there fully dealt with.

9.—SUMMARY AS REGARDS *G. MORSITANS.*

We have in *G. morsitans* a species which is more essentially bound up with the savanna than any of the other tsetses; for, while these all breed and shelter primarily in thicket, *G. morsitans* uses this only under special conditions and mostly performs these functions under such conditions as the savanna itself affords. The types of savanna of its choice are the most widespread which occur in Africa south of Kilimanjaro. Consequently this tsetse covers more country than any of the other species, with the possible exception of *G. pallidipes*, which overlaps all the others. The main habitat of *G. morsitans* is the miombo, and within this it needs a combination of vegetational types to satisfy its various demands. It requires principally (*a*) savanna of sufficient shade value, and with sufficient logs, rocks, or tree rot holes to form a good rest-haunt and breeding-ground, and (*b*) relatively open glades or plains in which to hunt for its prey. The degree in which these glades and mbugas are interspersed in the general wooding, and the extent to which the latter or the margins of the glades retain enough shade and food animals through the year, determine the distribution of this fly in the late dry season.

The hunger of this fly has been shown to correspond with the saturation deficit and the evaporative power of the air, and the density of its population falls or rises about a month after these factors have left (in either an upward or downward direction) an ascertained optimum zone. In the late dry

season, with these factors made fiercer by the desiccatory effect of the grass fires, existence becomes difficult for the fly. Depending on the conditions at the glades and mbugas, it may maintain a general hold on the country, or it may, in this season of stress, be found to evacuate much of it and concentrate in the sites that remain suitable. This late dry-season phenomenon of evacuation and local concentration is more marked in *G. morsitans* than in any of the other tsetses and offers added hope for its control. The prospect of control is hopeful in any case owing to the attachment of this species to a savanna type which in much country at least is essentially a vegetational sub-climax and which, through the removal of the bar to the further advancement of the succession by the cessation of grass fires, becomes so changed as to be unsuitable for this fly. Owing to its special attachment to the savanna, *G. morsitans* is more completely a "game" fly than perhaps any other species excepting *G. swynnertoni*.

10.—THE ECONOMIC IMPORTANCE OF *G. MORSITANS* AS DEDUCED FROM OBSERVATIONS IN TANGANYIKA AND FROM ITS DISTRIBUTION.

G. morsitans is a most efficient carrier both of nagana in animals and of the most virulent form of sleeping sickness (*Trypanosoma rhodesiense* Stephens & Fantham) in man. It is true that, as in malaria, human infects have usually to be present to start an outbreak of sleeping sickness, but, following the conditions of movement brought about during the war, the greater part of the Western Province of Tanganyika has been involved in an epidemic of the disease (now in hand through the concentration of the population), while lesser outbreaks or cases have occurred elsewhere which have been the work of this species of tsetse. And *G. morsitans* has carried this disease in the Sudan, in Nyasaland, Portuguese East Africa, and Northern and Southern Rhodesia.

As regards distribution, *G. morsitans* is absent from Somaliland, Kenya Colony, and Zululand; it is of importance in the Sudan and from there it throws an arm across to west Africa where it exists in its form *submorsitans* (Newstead). It occurs as small belts in Uganda, the southernmost of which enters Tanganyika Territory and there expands into the western, or Tabora, belt of 900,000 square miles to which so much reference has already been made. In Tanganyika, *G. morsitans* alone infests probably half the country; it is equally important in Northern Rhodesia, and fills a great proportion of Portuguese East Africa; and in Southern Rhodesia and Nyasaland it has been responsible for great invasions of country in the past twenty years. It formerly existed in the north-east of the Transvaal and the cause of its disappearance is disputed. It exists in the Belgian Congo (Katanga District; Lualaba river; Lower Kele), and the Bechuanaland Protectorate (Mababe). It excludes cattle practically wherever it occurs, though in two small localities in the Sudan the cattle appear to have become habituated to the local strain of trypanosome and die when placed elsewhere in "fly." The readiness to attach itself to human beings, in which it excels all tsetses except *G. swynnertoni*, makes *G. morsitans* most dangerous to man; while the vast extent of its habitats has enabled and will continue to enable sleeping sickness to go long undetected, and makes it certain that we cannot leave the fly alone till the expansion of population wipes it out. No tsetse is of greater importance, and of none have the studies of our Tsetse Research Department in Tanganyika been so full. It is very important now to pass on to large scale field experimentation to test all possibilities of exterminating this species.

F.—THE RELATION OF *GLOSSINA SWYNNERTONI* AUSTEN TO ITS INANIMATE ENVIRONMENT.

1.—THE VEGETATIONAL TYPES WHICH *G. SWYNNERTONI* CANNOT INHABIT.

The enormous areas under miombo (*Isoberlinia–Brachystegia* *) can be left out of account completely, for although *G. swynnertoni*, a dry-country fly, may enter and use their margins for a mile or two inwards, and may do so (freely) in small enclaves of miombo in thorn-bush, it does not inhabit them continuously.

Of large dense thickets † only the margins appear to be used, though Burtt's results for *G. morsitans* in Kazikazi (p. 315 below) probably apply here also. The thickets artificially created in Shinyanga, though not yet impervious, are giving a very high degree of protection to roads.

It will be seen further that where the fly population is greatly reduced, it evacuates large pieces of savanna bush on eluvial ground which, when in numbers, it inhabits, and concentrates on the drainage lines.‡

A somewhat open type of *Commiphora Schimperi–Combretum Zeyheri–Acacia stenocarpa* wooding occurring at 6,000 feet in Mbulu, relatively devoid of breeding-grounds and thickets, is apparently only seasonally infested.

" Large tracts of bush consisting of small, compact thickets with *Sanseviera* below, growing on semi-alluvial soil . . . are practically fly-free, although in contact at various points with fly-infested bush, notably the thick fly of the Chawasagugu–Kikome hills. It would appear that such small thickets cannot support *G. swynnertoni* unless occurring together with savannah trees " (Jackson, Musoma report, 31.x.1933).

In the large thickets, with large open spaces between, and no trees, up a hill, the lower slopes of which carried savanna wooding and replete *G. swynnertoni* in moderate density, the flies were extremely scarce (*ibid.*).

Finer differences have in any case yet to be learned. Thus in the southern Musoma belt " the investigator is continually alarmed by the contact of fly with apparently suitable but as yet uninfested bush," yet the present distribution of tsetse is of very long standing (*ibid.*).

Open country (pl. 2) is avoided, as by all tsetses, except for objects within visual reach in its margins.

2.—THE VEGETATIONAL HABITAT OF *G. SWYNNERTONI.*

(a) General description.

The dry thorn-bush or nyika (*Acacia–Commiphora–Ostryoderris*–other genera), to the relatively arid conditions associated with so much of which *G. swynnertoni* is adapted, presents a very different picture from the miombo of *morsitans* (pl. 1; pl. 3, fig. 2; pls. 5, 13, 14 & 15).

In the greater part of the great dry thorn-bush association there is no general canopy. Trees and groves of all heights, shapes, and sizes, and thickets of all sizes and densities, are scattered, often sparsely, sometimes more closely, through a land of grass which except in extreme conditions of dryness is usually closer and taller than that which commonly grows under miombo. The one respect in which the genera which dominate this type of country agree is, with a few important exceptions, their thorniness. *Acacia*, *Commiphcra*, *Balanites*, *Fagara*, and the trailing Combretums, carry thorns or spines. The

* See fig. 8. † See pl. 12, fig. 2. ‡ See pl. 13, fig. 1.

tree-Combretums do not; nor does the Baobab, which, sparsely scattered, is a characteristic feature; nor do most of the trees in an important community, referred to on this page, which is dominated commonly by *Ostryoderris Stuhlmannii*, *Commiphora Fischeri*, and *Combretum Zeyheri*. The thorn-bush, however, as stated already, is the name under which these varied, associated, and often very intermingled types are most commonly known in east Africa and seems best to describe them collectively.

The *Ostryoderris–Commiphora* community mentioned above is, over much country, the thorn-bush equivalent to miombo. Both characterise the eluvial ground; but there is the following difference. In the miombo areas, the plain eluvial soil marches on over great tracts with mere valleys and glades interrupting it. The miombo wooding is, therefore, able to march on evenly also; but in the dry thorn-bush area a limonitic, iron-oxide, " marram " crust, commonly, but wrongly, called laterite, has formed by concretion just under the surface of the soil over very large areas of gently sloping eluvial. This interferes with the drainage, producing over-wetness in the rains and intensified drought in the dry season, and brings up on to the slopes plant communities which usually favour, more or less, the alluvium, in which this contrast of inundation and drought occurs normally in varying degree. Thus it comes about that the Acacias and Albizzias and their associates, which in the miombo country are confined to the glades and alluvial valleys, may be found everywhere in the dry thorn-bush country, mingling with the eluvial communities proper in this country where the crust is probably incomplete, or replacing them in country where it is probably not.

Another phenomenon common in much of this country, but more rare in the miombo, is the presence in the stratum overlying the granite, but underlying the soil, of a white cementing material which binds the decomposed rock and the soil about it into a concrete-like hard-pan. This may in Shinyanga be in part a marly deposit under an old southern arm of Lake Victoria, in part deposition of lime carbonates. Where either it or the iron comes near the surface, naturally or through erosion accelerated by man, a profound effect is produced on the vegetation, both wood and grass, which favours *G. swynnertoni*.

(b) Sub-divisions of the thorn-bush.

(i) *The wooding on the eluvial ground of the slopes and rises.*

The *Commiphora–Ostryoderris* community, already referred to, characterises, over much country, the well-drained red sandy loam soils, derived (*inter alia*) from schist, which ferruginous crusts and marly or lime cements have not shallowed. Thickets, dominated mainly by *Abrus Schimperi* and *Markhamia acuminata*, are common, though least so where grass fires are fierce.

The community occurs also strongly on the better-drained granite, but these eluvial granite slopes often carry very mixed wooding owing to a pocket-like distribution of the drainage—of moisture and drought—which results both from a broken limonite layer and from the varying positions and sizes of the large rocks under the ground. The result on the vegetation is given below.

In Musoma, " broadly, the savanna areas, as far as concerns the eluvial soils at least, range from nearly pure *Combretum ternifolium* through all intermediate grades to nearly pure *Acacia hebecladoides*. Both types may or may not include a large admixture of *Acacia stenocarpa*, *A. Benthamii*, *Lonchocarpus capassa*, *Sclerocarya Birrea*, and thickets of *Harrisonia*, *Rhus*, *Grewia*

and, sometimes, *Acacia pennata.* In some areas compact thickets containing *Sanseviera* are a characteristic feature, scattered at short and regular intervals through the open savannah woodland. The tops of the higher hills are frequently almost bare, recalling those of Ankole; there may be a scattered growth of *Combretum ternifolium* " (Jackson, 31.x.1933).

It may be remarked here that farther south *C. ternifolium* is confined to edges of mbuga or to small, seasonally swampy, pockets in miombo.

(ii) *Mixed wooding, eluvial and alluvial.*

An eluvial slope on which natural cementing processes or the erosion resulting from native cultivation has placed the soil surface at a short distance only above rock or the concretions referred to above, may carry mainly *Acacia* of species characteristic of alluvium; much of the purer *Acacia* country about old Shinyanga is wooding of *A. Benthami* and *A. spirocarpa* on eluvial soil a foot or two deep overlying the ferruginous crust referred to above. On granite slopes of the mixed kind referred to above will be found the eluvial elements, such as *Commiphora Fischeri*, *Abrus* and the Markhamias, cheek by jowl everywhere with flat-topped Acacias (*A. spirocarpa*) and even gall-acacias, *Lannea humilis*, and patches of the hard-pan grasses. Typical hard-pan vegetation (poor *Microchloa indica* grass, *Commiphora Schimperi*, *Lannea humilis*, etc.) has been found on this soil over rock on the top of a kopje. Broken or incomplete iron crust produces the same mixed conditions. The effect on the tsetse is considerable as regards the provision of the contacts that it needs.

(iii) *The vegetation of the alluvium.*

What has been written of the alluvium under *G. morsitans* (*see* p. 60 above) applies broadly here too, except that forms of the white hard-pan seem especially to underlie the dry thorn-bush alluvium and to play an outstanding part in the life of *G. swynnertoni.* The following are some of the communities occurring on the black alluvial soils and those permeated with the white cement.

(α) *Community* (α).

This consists of black-soil mbugas * which are swamped in the rains, but dry out completely through cracking in the dry season. These † traverse the country as drainage lines or form great plains or " sunk-lands " that sometimes (as in the case of the Wembere Plain) fill the sites of old lakes. Great parts of them carry grass only, but woods, small or (as on the Huruhuru) very extensive, of nearly shadeless gall-acacia may be a prominent feature.‡

(β) *Community* (β).

Where erosion has set in, the streams which flow in heavy rain from the outlets of the mbugas have formed channels, and these are cutting back through the mbugas. The soil is becoming drained. Amongst the earliest immigrants, with drainage still very incomplete, are, under certain conditions, the small " ray-acacias," *i.e.* Acacias with branches radiating thickly from a base near the ground. Of these *A. Kirkiana* may, for ready identification, be referred to as the " green-barked ray-acacia " and *A. Stuhlmannii* as the " hairy ray-acacia." They grow in dense woods, large or small.

* See pl. 4; and pl. 13, fig. 2.

† These seasonally-wet grass-lands are marked " SSG " on the game map.

‡ See pl. 12, fig. 1; and fig. 32.

Acacia pallens ("knobby-thorn acacia" or mkambala) forms often very extensive woods on more or less rich black plains undergoing their early drainage. It also occurs at more advanced stages. The small-tree "wait-a-bit acacia" (*A. mellifera*, called murugara), with serried hooked thorns, occupies the edges of mbugas which are still seasonally wet. Palms (*Hyphäene*) sometimes occur on this boundary between communities (α) and (β). The fine *A. usambarensis* (the "stink-bark," so called owing to the garlic smell of its bark which is much used for cordage) begins to occur here. Both *A. pallens* and *A. usambarensis* occur best developed under miombo-climate conditions, on extensive alluvial enclaves in the general miombo-clothed alluvium or covering alluvial areas independently under this climate, as between Dar-es-Salaam and Kilosa. They rank there as part of the mesophytic savanna and form a home for *G. morsitans*. In the dry thorn-bush, *Acacia senegal*, *A. spirocarpa* (pl. 4, left & right), and *A. rovumae*, all begin to appear. The first-named (pl. 5, fig. 2) occurs also on hard-pan.

(γ) *Community* (γ).

Aided often unintentionally by human agency, erosion has cut old alluvial deposits into slopes and banks by means of branching dongas, thus greatly improving the drainage. This type of country is very widespread both in the thorn-bush area and in the broader valleys of the miombo. In common with colluvial interzones it is sometimes called "semi-mbuga."

Acacia rovumae (the fluted Acacia or mgongwa), a tall tree, more or less flat-topped, over-topping scattered thickets and low *Commiphora* woods but itself widely-spaced, usually occurs here. It is particularly extended in its incidence and is probably the chief *Acacia* dominant of the thorn-bush of the Central Province. The chief Albizzias of the thorn-bush, *A. Harveyi* and *A. sericocephala*, and some of the trailing Combretums (*C. purpureiflorum*, *C. obovatum* and *C. trichopetalum*) are found here, and *Dichrostachys glomerata* and *Ormocarpum trichocarpum* are particularly common. Some of the Acacias which figure earlier extend also into this community. *Acacia spirocarpa* (the umbrella Acacia or mgunga) is included, but over large areas it is also associated as a fine but widely-spaced tree with conditions merely of climatic drought. *Balanites aegyptiaca* (which is useful in relation to Bilharzia disease) often mixes as a dominant with sparse, large, *A. spirocarpa* in dry country which is otherwise nearly open. This includes some of the lava tracts near Arusha and over our northern border.

An effect of this kind of erosion may be referred to here. Where the erosion channels have cut down to bed-rock, eluvial woodland communities may be found colonising the latter. They may thus be present both on the heights and at the bottom of the valleys with alluvial communities between. An example of this is provided by the miombo near Kilosa. This, and the early leaf-flush associated with the lower situation, is not without its effect on the local habits of the tsetse.

A group of so-called semi-mbuga type that comes partly here, partly in community (δ) below, is one often dominated by *Dalbergia melanoxylon* (mpingo or African ebony) and its associates. It includes (as at Lubaga *) a type of soil as black as the black-soil mbuga but better drained and more granulated, with travertine nodules, which is much in demand for cultivation and is one of the best soils for cotton in Tanganyika.

* See fig. 4.

(δ) *Community* (δ).

Conditions which favour the *Commiphora Schimperi–Lannea humilis*–Gall-acacia hard-pan community have occurred. Much of the soil of the thorn-bush country, in Usukuma at least, overlies the white hard-pan cement already described. Where this soil has worn thin through erosion, and the cement is therefore (or naturally) near the surface, the soil is a bog during heavy rains, but, being apparently permeated from below with the cementing element, becomes almost like rock in the drought. It supports sparse, poor grasses in miniature tufts (*Microchloa indica* and a *Sporobolus*), and its wooding is an open and sparse one of trees and clumps mainly of *Commiphora Schimperi* (Mponda) and *Lannea humilis* (Mtinji), but also of the gall-acacias. The scattered thickets which bound it or grow on slight rises within it, or follow the drained banks of storm-streams and erosion channels which bisect it, are dominated by a shrub-*Combretum* with smooth, pale bark—the so-called mlowashi, *C. parvifolium.* Larger Acacias than the gall-thorns (*A. mellifera, usambarensis, Fischeri, senegal,* and *rovumae*), *Terminalia Stuhlmannii* and, especially, the Albizzias (*Harveyi* and *sericocephala*), are often present also or are sandwiched within hard-pan patches and strips. The latter form shallow, branching drainage lines * through the thorn-bush or fringe in varying width the black-soil mbugas and the courses of the seasonal streams. They are much more open than the general woodland which hems them in, both as regards tree density and shortness of grass, and, as is shown below, are a concentrating point for the tsetses.

In some places, probably as the result of maltreatment by native settlement, since the process can be seen in progress to-day (pl. 19), the hard-pan has been reached very generally. It is practically bared over an area of perhaps 50 square miles in Blocks 9 and 10A at Shinyanga, which is covered by an open wood consisting (mainly) of *Commiphora Schimperi* and *C. subsessilifolia*, with *Lannea humilis* and small hard-pan thickets; "drier," eluvial elements on old ant heaps and low rises run through it. It will be seen below (*a*) that hard-pan is the one element in the vegetational make-up which in Shinyanga is absolutely essential to the existence of *G. swynnertoni*, and (*b*) that it is also the element from which it is most difficult to expel this species. Thus, the more man maltreats the country, the more difficult is it for him to regain it once it is lost to this tsetse fly.

(ε) *Community* (ε).

On the banks of seasonal streams which have so grown that the sand in the channels of their past or present beds forms good reservoirs of moisture in drought, whether these occur in the thorn-bush or in the miombo, the tall trees *Acacia campylocantha* and *A. xanthophloea* appear in replacement of the drier riverine thicket. In damper country (as at Biharamulo and in parts of Uganda) the first of these Acacias may even leave its stream-banks and occur scattered over eluvial hill-sides, but the conditions which enable it to do so turn this into *morsitans* country, in which *G. swynnertoni* will not live.

(ζ) *The relations of the Commiphoras and Acacias, and of the Combretums with the Commiphoras, Acacias and the miombo.*

In a wood such as that on the hard-pan in Block 9, referred to above, Acacias are sparse, though Albizzias are common; the Commiphoras (*C. Schimperi* and *C. subsessilifolia*) dominate completely. At the opposite extreme, *i.e.*

* See pl. 13, fig. 1.

on the best and most uniform eluvial, the same thing happens; other Commiphoras (*C. Fischeri* and *C. ugogensis* with their associates) exclude all but a sprinkling of Acacias. In general, there is a segregation between *Commiphora* and *Acacia* like the patches of a patchwork quilt, but *Acacia* is seldom absent from the larger *Commiphora* patches or the latter from those of *Acacia*, and very commonly, both on the broken granite and on marram, there is the minute admixture referred to already. Elsewhere, woods of *Commiphora* form an understorey to taller, wider-spaced *Acacias* (such as *A. rovumae*). The tree Combretums (*Zeyheri*, *apiculatum* and *splendens*, but mainly the first) are very abundant in the dry thorn-bush, particularly on eluvial soil in conjunction with *Ostryoderris* and its associates, though they occur also elsewhere. They are, however, with *Combretum Fischeri*, equally abundant in miombo wooding on eluvial. They also form communities by themselves on some of the lower hill-sides (as at Kikore), or in the form of an interzone between miombo and seasonal swamp (as on the edges of the Mkata plain). It would be unwise to use them in our classification of woodland types until their ecology has been more fully worked out. Any reference to *Combretum* must distinguish these tree-Combretums from the trailing species listed above under community (iii) with their better defined requirements.

3.—THE USE MADE BY *G. SWYNNERTONI* OF THE SEVERAL PLANT COMMUNITIES WHICH MAKE UP ITS VEGETATIONAL HABITAT.

This species resembles *G. morsitans* in needing more than one kind of country and in concentrating where the types which it requires come into contact or combine.

(a) Early observations.

It had been noted as early as 1922 (Mwanza) and 1923 (Shinyanga) that the females of *G. swynnertoni* come to man in far greater numbers in mbugas than in the general bush (Swynnerton, 1923 : 332), and that the fly density on roads and on the edges of mbuga was far greater than in the bush away from such places (diary of September 1923). It was suggested at first (of the mbuga flies) that they were hungrier because few game animals were noted to be present in these particular cases, but Jackson (who greatly amplified the above observations for *G. swynnertoni* also) explained the matter by proving that tsetse came to such places because they were hungry, instead of being hungry because they were there. Thus, open mbugas and roads are *G. swynnertoni*'s feeding-places, as they are those of *G. morsitans*.

The position at the hard-pan patches and strips still needed explanation. Here the flies are present also in very great numbers, but neither the hunger average nor the percentage of females is anything like what they should be at a feeding-ground.

Again, what represents for this fly the essential home, in which it shelters and breeds? Actually the species had been found breeding mainly in thickets but also under rocks (in great numbers) and under logs when available.

We know much more to-day. Potts, Jackson, Lloyd, and more recently, Vicars-Harris, have all worked on the habits of this fly. Lloyd carried out in Shinyanga from December 1930 to July 1932 a well-planned and useful investigation. As it has just been published * it is not proposed to re-state much of its detail here; but the following was the general outcome.

* Lloyd, 1935, *Bull. ent. Res.*, **26** : 439–468.

(b) The use made of the different bush types.

Lloyd compared (in all) four vegetation types in Shinyanga and three more in Musoma. Flies in (1), typical eluvial *Commiphora Fischeri-Ostryoderris* wooding with thickets, were replete and the female percentage was small, indicating rest-haunt or " home " conditions. In (2), open short-grass hard-pan with thickets, neither average hunger nor female percentage was high, but they were higher than in (1) " and slightly higher than those of fly caught in the home of *G. morsitans* " : indicating intermediate conditions and flies. In (3), nearly thicketless, short-grassed *Acacia spirocarpa,* both were high but density was low, where there was no hard-pan admixture. These are feeding-ground conditions. In (4), open plains of black alluvium and hard-pan, both females and hunger were very high. These are typical feeding-ground conditions. In (5) and (6), *Acacia–Balanites* communities with thickets, one with long grass, one burned, the flies were by no means hungry and the female percentage was low. These were rest-haunt conditions. In (7), nearly thicketless open *Acacia* (*spirocarpa, Fischeri, Benthami, hebecladoides* and *Seyal*), they were hungry and the female percentage was higher. These approach to feeding-ground conditions.

In Musoma Jackson took four thorn-bush communities, varying in their composition (which he described in some detail), and for each at the same time a more open control close by. Each of the former showed comparatively high densities of replete male *swynnertoni,* while the controls showed a greater or less approach to a feeding-ground composition and condition of the flies taken. They were as follows :—

(1) Small compact thickets, usually with a large central Candelabra *Euphorbia,* and always with a rather dense growth of *Sanseviera* below, interspersed in savanna of *Acacia hebecladoides, A. Benthami, Dicrostachys glomerata, Ormocarpum* sp., *Lannea humilis,* and *Randia Taylorii.* The thickets themselves composed of *Rhus, Grewia,* and *Acacia pennata* (Chamliu area).

Flies 38 per hour; mean hunger stage 3·22; female % 9; young % 14.

Control, in the drainage valleys below :—

M.H.S. 3·68 (hungrier); female % 15; young % 26.

(2) Savanna of *Acacia hebecladoides, Commiphora pilosa, Dalbergia melanoxylon* and a few *D. Stuhlmannii, Fagara, Lannea* spp., a few *Ormocarpum,* and *Combretum splendens* and *C. ternifolium.* Thickets of *Harrisonia,* with some *Grewia.* Grass growth rather scanty, with numerous bare patches of red soil (Suguti river area).

Flies 131 per hour; M.H.S. 2·81; female % 2·5; young % 1·7.

Control, in the *Acacia Seyal–A. hebecladoides* interzone below :—

Flies 50 per hour; M.H.S. 3·08; female % 6·5; young % 8·7.

(3) Very mixed savanna of *Acacia stenocarpa, A. nefasia, Combretum splendens, Commiphora pilosa, Lonchocarpus capassa, Dalbergia Stuhlmannii, Phyllanthus Engleri, Randia Taylorii, Dichrostachys, Ormocarpum* and *Albizzia,* with thickets of *Harrisonia, Rhus, Grewia,* and *Acacia pennata* (Chamliu–Maji Moto area).

Flies 56 per hour; M.H.S. 2·93; female and young % 0·0.

(4) Savanna dominated by *Lonchocarpus capassa,* with subsidiary trees of *Acacia Benthami, Commiphora Schimperi, Lannea* sp., *Sclerocarya Birrea, Dalbergia melanoxylon,* and odd *Acacia spirocarpa.* Very little thicket, but a

few bushes of *Grewia*, and a very few *Harrisonia* and *Acacia pennata* (Baridi hills area).

Flies 60 per hour; M.H.S. 2·71; female % 0·0; young % 5·0.

Control, in open savanna of *A. spirocarpa* on alluvial soil below :—

Flies 22 per hour; M.H.S. 3·11; female % 9·1; young % 9·1.

Large fly-marking experiments, in January–February 1931 and March 1932, formed part of Lloyd's investigation and from these it was found :—

(α) that the flies were feeding just as much in the hard-pan as outside it; it was a feeding-ground as well as a home, or in Jackson's words, " a hotel, not a restaurant," and a situation " in which the fly population spends all its time in its feeding-grounds if these happen to provide the requisite conditions."

(β) that the flies would move as readily from one piece of hard-pan to another as to a road feeding-ground, and that " if they strike a road or other feeding-ground before meeting an animal, they will patrol this until they get a feed and then retire to less exacting conditions in well sheltered bush."

(γ) from a comparison, by means of 3,386 marked flies, of the respective rôles of *C. Fischeri–Ostryoderris*, open *Acacia* wooding, and hard-pan, that the relation of the first to the second and third was that of a " home " to feeding-grounds; thus the more replete flies marked in *Commiphora Fischeri* took longer to reach the hard-pan than did the hungrier individuals.

(δ) that there was a strong tendency on the part of flies marked in the *C. Fischeri* to remain in the hard-pan when they got there. There was no marked reciprocal behaviour by the flies in the hard-pan. Thus if the population is diminishing owing to a reclamation measure or to some other factor, the flies may, in effect, evacuate the *C. Fischeri* and be found almost exclusively in the hard-pan, as has actually happened in Shinyanga in these conditions.

Lloyd expresses the " preference " of the fly for the different types by means of the average number taken " per boy per hundred yards " during the period, December 1930–July 1932, as follows :—Hard-pan 5·4, *C. Fischeri* 1·2, *Acacia* 0·9, old cultivation 0·4. He concludes that *C. Fischeri*, *Acacia*, and hard-pan, are all capable of supporting *G. swynnertoni* provided that food and shelter are present, but that the hard-pan, which always combines in itself openness, savanna-type shelter, and thicket for breeding and resting, is the most favourable and is capable in itself of supporting a population of this fly.

G. swynnertoni is commonest during the first month or two of the dry season. As the dry season progresses it decreases in numbers and reaches its minimum during the short rains. There is a rise in the short dry season following the improvement of conditions brought about by the early rains; after that numbers remain fairly constant until the end of the long rains. " Hunger and female percentage are least in the beginning of the break of the short rains " (Lloyd).

As regards relative suitability for breeding Lloyd found pupae and pupa-cases as follows :—

In hard-pan wooding,	19·6 per hour;
in *C. Fischeri*,	23·4;
on the interzone (border line) between *C. Fischeri* and the hard-pan,	79·4, including an exceptional haul;
the same,	20·4, excluding the " haul."

The remaining woodland communities have not been tested so intensively. The fly rounds now in progress in Maswa will, however, give information on communities which are absent from Shinyanga. Of a nearly pure, close, unusual, savanna stand of fine trees of *C. Schimperi* on red soil, Wheeler already reports that it produced practically no flies during the early rains of 1934–35, but that during that time the flies literally swarmed in open glades, on roads, and especially in old, partly regenerated but still very open, sleeping sickness clearings.

In my observations of May–June 1922 in Mwanza, with the rainy season just over, it was noted that " in general the fly was found in its largest numbers in mgongwa Acacias (*A. rovumae*) interspersed with considerable but broken thicket undergrowth, and in mhali wooding (*A. spirocarpa*), chiefly where there were thickets of a type that would have attracted *pallidipes*. . . . When thickets such as I have described as of the *pallidipes* type bounded a swamp, the presence of more or less numerous tsetse (*G. swynnertoni*) was nearly certain " (Swynnerton, 1923).

Few flies were taken anywhere in riverine wooding, although they might be present in numbers outside. This has been confirmed generally since, at any rate for most of the year.

The following is a summary of Lloyd's work and previous observations :—

(i) The flies when numerous inhabit all kinds of savanna wooding within the general range, except large areas of miombo, provided that scattered thickets are present. Where thickets are absent from a piece of country the flies are relatively scarce and become more so during the late dry season. Their requirement for breeding, and for refuge from desiccation and fires—in fact their rest-haunt during dry conditions especially—is thicket.

(ii) Their requirement for the finding of food, and doubtless as a refuge from excessive humidity, is open or relatively open country. Failing to find it in their " home " they visit in the course of their search, and wait beside, or more likely (as standing catches indicate) investigate, open mbugas, roads, and the hard-pan drainage lines. These contacts between bush and open country form sites of concentrations, temporary or more permanent (hard-pan). Open Acacia woodlands with the short grass which results from the presence of an underground iron crust are used also as feeding-grounds, and the flies in this case sometimes centre in the thicketed rocky bases of granite kopjes standing in them.

(iii) The hard-pan drainage lines, together probably with their contacts with the savanna woodland which comes down to them on either side, are a compendium of all the needs of the flies, at any rate for much of the year. They provide open ground with short, sparse grass and bare patches of ground, open savanna woodland, and numerous thickets which the grass fires hardly reach.* In these hollow hard-pan strips the hungry flies are found looking for food, and with them, in great numbers, are found the " fed " population, of which only the males appear and the collecting of which with the others produces a hunger-stage effect and a percentage of females which is intermediate between that of a typical " home " and that of a feeding-ground (pl. 13, fig. 2, and pl. 15, fig. 1).† The hard-pan is not a " restaurant " like the open mbuga and road; it is a hotel in, and beside,

* See pl. 13, fig. 1.

† See also Jackson's figures given above.

which the flies both dwell and feed. The flies cannot dwell in an open road or mbuga, though, leaving their base close by, they can search it for food; in this case therefore the savanna-plus-thicket home and the feeding-ground are separate but in juxtaposition with one another.

(iv) As the fly population becomes reduced the survivors concentrate more and more in the optimum, hard-pan habitat, the mechanism of which concentration has been shown by Lloyd to be a relative reluctance to leave it once they are there, at least during certain seasons. For season exercises a strong differential influence on the distribution of this fly, as observations by Vicars-Harris are now showing clearly.

(c) Furniture and ecidio-climate.

During part of the year at least *G. swynnertoni* breeds much on the thicket floors, but Vicars-Harris is finding that in the late wet season the largest numbers are under logs and at tree bases in the thickets, under rocks in kopjes, and in rot holes in trees as much as six feet from the ground, in any nooks, in fact, in which real protection from the rain may be had. Under conditions of non-burning (pp. 272–278 below), with moisture doubtless intensified in consequence through grassmat and thicket, the areas in which these drier sites are used appear to become circumscribed. Vicars-Harris suggests that it may not be a difficult or expensive matter to block with mud the breeding-sites in these areas only, and so to force the flies and puparia into conditions which may be too moist. This measure would amount to depriving the fly of an essential nook-climate. However, the particular observation here referred to requires confirmation over a larger number of seasons.

4.—THE PHYSICAL FACTORS.

(a) The geological and elevational habitats as indicators of physical factors.

In general, the range of the dry thorn-bush, and of *G. swynnertoni*, includes that of the granites and gneisses and their intercalated formations, where these coincide with a rainfall of less than 30 inches combined with a long and severe dry season and a short dry season during which the saturation deficit becomes great. Shinyanga, though near the upper limit of this rainfall range, becomes exceptionally dry at these times, largely because the prevalence of an impervious hard-pan not far below the ground-surface reduces the moisture-storing soil-layer. Evaporation rates as high as 90 c.c. obtain at four feet (Livingston atmometer, uncorrected). As stated already, the formation of a largely impervious ferruginous marram crust in the soil is also a very general phenomenon and leads similarly to excessive seasonal moisture and drought, in the rains and dry season respectively.

Thorn-bush and *G. swynnertoni* are found also on wide alluvial areas, such as that of the Mbarangeti and Rowana rivers, flowing into Speke Gulf, and that of the lava soils of the tertiary volcanics of Arusha.

As regards elevation, *G. swynnertoni* occurs at 6,000 feet in parts of Mbulu district and, it is thought possible, still higher in the country west of Lake Natron on both sides of the border. It obviously withstands cold as well as, or better than, *G. morsitans*. It is not known to occur at less than 3,000 feet, but there would appear to be no reason why it should not invade part of the lowlands of Kenya, between Voi and the coast, if its present advance to Moshi were eventually to bring it there.

Much of the country infested is undulating plateau. Taken as a whole,

it is by no means so well drained as that on which the miombo grows, but low rainfall and dry season soil aridity are general.

(b) The standard climate of Old Shinyanga and the round of the seasons.

The following account of the standard climate of Old Shinyanga, within fifteen miles of which most of our work on *G. swynnertoni* has been done, is extracted from a report by Vicars-Harris, who handles the meteorological observations at that station.

The station is on a reddish, eluvial, granite, grit soil, for the most part from two to five feet deep. Just exposed boulders stud the ground in groups and the soil carried, before clearing, vegetation of the mixed *Ostryoderris–Commiphora* and *Acacia* types referred to on p. 86 above as characterising "mixed" granite slopes.

(i) *Rainfall.*

Although it is doubtful if there is such a thing as a normal year, one might draw the following picture as the best type of season which from our records of the past few years one could reasonably hope for :—

A succession of three or four heavy showers in mid-October, followed by one or two heavy showers during November. The definite break of the first rains in the first week in December, then more or less daily rain till the second week in January, when the short dry spell sets in. Only one, or possibly two, heavy showers during the latter half of January and February. The second rains early in March and during April. These should continue into the latter half of April and then gradually fade away. One or two short but heavy showers in mid-September may in some years be expected. The periods and average rainfall would be approximately as follows :—

	Inches.
October–November, occasional showers, end of dry season	3
December–mid-January, first rainy season	10
Mid-January–February, short dry season	1
March to mid- or late April, second rainy season	12
May–September, long dry season	2
Average total rainfall	28

To expect anything better than this either in quantity or distribution is not justified by experience in Shinyanga; the season 1929–30 was a good year, but each year since then the rains have either ended abnormally early or have been defective otherwise.

(ii) *Air temperature.*

Generally speaking the monthly mean maxima are never above 92° F. or below 82°. The absolute screen maximum recorded is 97°. October is the hottest month; the first part of November is often hotter, but the monthly mean is brought down by the break of the small rains at the end of that month. The lowest mean maxima are recorded in the dry season (July to August) and during the rainy months.

(iii) *Minimum screen temperatures.*

As regards the minimum screen temperatures, July is the coldest month, though on two occasions August has shown a lower absolute minimum. The range is from 58°–60° in July and August to 65° in October and November. The absolute minimum recorded is 50°.

(iv) *Solar radiation.*

Solar radiation follows very closely the maximum thermometer and needs no comment except that a drop in the temperature coincides with the appearance of smoke haze, and that an immediate rise accompanies the first showers which clear the air. As regards monthly means, the range is from about 160° F. in October and March to approximately 145° F. in the height of the dry season.

(v) *Soil temperatures* (2 *p.m. readings*).

Soil temperature on the surface follows closely the curve of the maximum thermometer, except that the readings are more influenced by cloudy weather and rain, owing to the thermometer not being recording, so that if the weather happens to be cloudy or wet at the time of reading the result will be affected, whereas the recording maximum thermometer records any sunny periods before or after the actual time of the readings. The range in monthly means is from about 130° F. in the months of October and November to about 95°–100° F. in December and January.

The monthly means of soil temperatures at one foot below surface range from 79°–89°, the lowest periods being during the two rainy seasons and the highest during the latter part of the dry season. Short showers produce little alteration unless accompanied by several cloudy days, but heavy rain is recorded by large drops in the temperature, showing clearly the immediate cooling effect of rain on the subsoil.

Realising that young plants at Shinyanga have their roots in dry soil at a temperature of nearly 90° F. every day during the dry season, one ceases to wonder that it is difficult to get them to grow (*see* p. 297 below). While small shelters covering the plant reduce the surface soil temperature and prevent scorching of the plant itself by the sun, they probably do not influence the soil temperature at one foot.

(vi) *Relative humidity* (2 *p.m. readings*).

During the first rainy season (December–January) relative humidity at 2 p.m. is round about 60%. It drops usually to about 50% during the short dry season (February–March) and rises again during the second rains (March–April) to as much as 70% in a normal year. In a year like 1934 the humidity declined in a steady curve from less than 60% in January to the low thirties in July to September. The monthly mean humidity has never been below 29% or above 71%. These figures, being worked out from readings at 2 p.m., are mainly of value in that they give the humidity during what must be almost the driest period of each day and that which would be the most trying to the tsetse if it were deprived of the means of evading it. Our thermohygrograph readings will give a better picture of the humidity through the day, night and seasons, but records from them are not yet available for a whole year.

(vii) *Evaporative power of the air as measured by Livingston atmometers.*

During the past two years the mean monthly evaporation rate has never fallen below 35 c.c. per day, but in 1931 and 1932, which were more normal years, the rate fell during the big rains to about 25 c.c. per day. One may take it therefore that in normal years the range would be from 25 c.c. during the rainiest month to approximately 90 c.c. during the late dry season. The graph shows a very regular curve, low during the first rains in December and January, with a small or medium rise during the short dry season in

February (or in some years January) to between 40 c.c. and 50 c.c., thence a fall down to 25 c.c. or thereabouts during the big rains in March and April, and from there a gradual rise in a steady curve to about 90 c.c. in October and November.

(viii) *Duration of sunshine.*

The records show a monthly mean range of bright sunshine from 9·5 hours a day in July and August to 6·0 hours a day in March and April. While a maximum monthly mean of 9·5 hours in July may seem low to anyone knowing the almost continuously cloudless skies of the mid-dry season, it is explained by the fact that, looking down the daily readings for these dry-season months, one sees the great predominance of readings of 10·5 hours or 11 hours counteracted in the monthly means by readings of 2 or 3 hours only on an occasional cloudy day. Similarly during the rainy spells, the generally low readings of the majority of the days are affected by an occasional reading of 10 hours or more during a temporary break in the rains. Vicars-Harris describes the daily sunshine to be expected during the various seasons (in Tanganyika) as follows:—

October–November . .	9 hours.
December–mid-January .	5–6 hours, with days of 10 hours between rainy periods.
Mid-January–February . .	6–7 hours during the end of January, with a rise to 8–9 hours or more during the short dry season.
March–April	4–5 hours, with days of 10 hours between rainy periods.
May	7–8 hours.
June, July, August, September	10–11 hours.

(ix) *Wind.*

The range of wind is from a daily average of 1·2 m.p.h. in the rainy seasons to 3·8 or 4 m.p.h. during August and September. These figures do not give a correct impression of the winds experienced at Shinyanga and are explained by the fact that any average over 24 hours includes many hours of practically no wind at all. Take for example a dry-season day. From midnight to dawn there is usually only a very slight breeze or no wind at all. From dawn to 8 a.m. the velocity ranges from 4 to 7 m.p.h. (2 on the Beaufort scale). From 8 a.m. to 12 noon it gradually rises from 9 m.p.h. or so to 18 or 20 m.p.h. (3 to 4 on the Beaufort scale), with gusts of greater velocity. From noon to sunset it gradually dwindles from 16 to 18 m.p.h. to nothing or light air (from 4 to 0 or 1 on the Beaufort scale). From sunset to 8 p.m. it is usually calm. From 8 p.m. to 10 p.m. or slightly later the wind rises to from 16 to 18 m.p.h., again dropping to calm from 10 p.m. to midnight. From this it will be seen that one can roughly divide a normal dry-season day as follows :—

	Wind velocity (Beaufort scale).
Midnight to 8 a.m.	0–2.
8 a.m. to 12 noon	3–4, with gusts of from 5 to 6.
12 noon to 8 p.m.	2–0.
8 p.m. to midnight	4, dwindling to 1–0.

There are thus about 18 hours with the wind ranging from 0 to 7 m.p.h. and only 6 hours with the wind ranging from 15 to 18 m.p.h. This refers to a

typical dry-season day. Then, every month, there are odd days with no wind at all, which bring down the monthly average of daily means to the figure of about 4 m.p.h.

During the rains, the winds are much more irregular and the figures are affected by strong winds of from 20 to 30 m.p.h. before and during storms, while during the greater part of the day there is only calm to light air.

(x) *Summary of the standard climate as measured at Old Shinyanga.*

In conclusion Vicars-Harris draws a picture of a typical dry-season day and of a typical rainy-season day, from readings at 2 p.m.

	Dry season.	Rainy season.
Relative humidity	35%	60%
Dry bulb	89° F.	80° F.
Screen maximum	90° F.	81° F.
,, minimum	58° F.	62° F.
Solar radiation	160° F.	145° F.
Soil thermometers, surface . . .	135° F.	100° F.
,, ,, 1-foot	88° F.	79° F.
Evaporation	90 c.c.	25 c.c.
Wind (average over 24 hours) . .	4 m.p.h.	1·5 m.p.h.
Sunshine	11 hours	6 hours

(c) Some eco-climates of *G. swynnertoni* at Shinyanga.

Our full work on the eco-climates of *G. swynnertoni* is only commencing. Lloyd, however, carried out atmometer readings in three plant-communities much used by *G. swynnertoni* during a period of fourteen months. His figures are shown in the following table :—

TABLE 9.

Evaporation rate, in cubic centimetres, in hard-pan, riverine thicket and *Commiphora Fischeri* bush on the Wajimira stream in Block 11, Shinyanga, Tanganyika Territory. Monthly average.

Year and month	Hard-pan	Riverine thicket	*Commiphora Fischeri*
1931			
May	44·09	20·91	29·00
June	51·44	30·39	34·29
July	55·63	34·21	39·55
August	60·61	45·62	55·19
September . . .	66·93	48·20	61·20
October . . .	68·29	55·35	70·94
November . . .	61·09	46·51	63·48
December . . .	24·97	12·58	28·69
1932			
January . . .	43·06	21·54	36·97
February . . .	33·45	16·75	29·00
March	30·31	14·56	27·42
April	39·03	15·89	23·69
May	52·63	20·37	42·56
June	67·14	29·53	53·55

An interesting point to which Lloyd draws attention is that the evaporation was higher in the hard-pan than in the *C. Fischeri* area till October, when, and till the end of the year, it became slightly higher in the latter.

The standard climate as measured in an open spot in a Stevenson screen is totally different from the eco-climates which the fly encounters in the variously-shaded or exposed situations to which it resorts in different seasons and at different hours; for an insect that settles so much on open ground the figures for the surface soil thermometer must represent the actual temperature conditions which it there encounters.

5.—THE EFFECT OF SEASON AS CAUSING CONTRACTION AND SHIFTING ON THE PART OF *G. SWYNNERTONI*.

(a) Dry-season contraction.

There is a strong tendency in the late dry season to evacuate areas containing no thicket. The relative slowness of the eastward invasion of the *swynnertoni* fly belt of the Barabaig country in Mbulu is believed to have been due to a scarcity of thicket on much of the front lately reached. No such large seasonal evacuation of country has been seen to take place as occurs sometimes on the part of *G. morsitans*, probably owing (usually) to the presence of thickets.

(b) Wet-season selection of habitat.

Nash called attention to the fact that a concentration was taking place on the part of *G. swynnertoni* when *G. morsitans* was dispersing, and *vice versa.* He described this theory in his paper of 1930 (p. 152), and graphs made by Vicars-Harris from the various types of vegetation community represented on the fly rounds at Shinyanga, with observations which he has made in Shinyanga and Maswa, have lent conviction to the view.

It is certain that to avoid deleterious extremes of temperature and humidity and to retain continuously the eco-climates most favourable to them, the tsetses must alter their station with the season. In this case, the present observations strongly promise to show that an intensive concentration of *G. swynnertoni* takes place in the more open, short-grassed, hard-pan during the rains and that it is dispersed very largely during the dry season into the closer vegetational communities; that each of these other types has its period or periods of maximum popularity in orderly succession when the short grass hard-pan is not holding the bulk of the fly population; but that where the hard-pan carries plenty of thickets and the communities on the eluvial soils adjacent have become densified through not burning the grass, the hard-pan concentrations persist. The observations cover closely a period of only twenty-eight months so that fuller confirmation is needed. This may be regarded as having been obtained since the above was written. Vicars-Harris is about to publish a valuable paper on the subject which will be further interesting for Burtt's descriptions of the vegetation.

Jackson found in Musoma that *G. swynnertoni* was confined to eluvial or semi-eluvial soils with at least a low minimum of thicket—lower than our observations in Shinyanga had suggested to be necessary; the climate, however, in Musoma, is moister and game blood is more readily available, and Jackson found also that close growth in the savanna trees (*Acacia hebecladoides* especially), such as that near the Suguti river and about the Baridi hills, appeared to form a substitute for thicket.

In 1933 I found *G. swynnertoni* present as a "mixed" population and the females larvipositing at the foot of the Acacias well away from thicket in

the open savanna wooding at Banagi in the Serengeti Plains. But game was in very large numbers and, also, the month was December.

6.—THE EFFECT ON *G. SWYNNERTONI* OF GRASS FIRES.

(a) The effect of the ordinary annual grass fires.

The destruction of the herbaceous soil-cover by the grass fires leaves a bare earth surface which hurls back the heat of the sun and contributes very greatly to the desiccating power of the air during the late dry season. The hunger of the flies is increased much at this time, like that of *G. morsitans*, and there is no doubt that the great drop in numbers towards the end of the year is not merely an activity effect, due to the easing of thirst brought by the early rains, but is in part also the sequel of a destruction of flies through thirst which accentuated desiccation had produced. At the same time visibility is much increased and the flies are favoured thereby, while, locally, eco-climates persist that enable some flies to survive.

(b) The effect of organised fires late in the season (September).

In the usually good grass country with which this fly is associated, the effect of organised fire late in the season (pl. 14, fig. 2) is (i) to produce a drive of the flies before the fire; (ii) to burn through the smaller thickets which might have offered them a refuge and destroy pupae therein; and (iii), especially, to accentuate still further the desiccatory effect just referred to. The hard-pan strips continue to save the flies from complete expulsion, burning, as they do, very lightly indeed and patchily, unless they are cleared of the thickets and trees standing on them. The thickets within them are hardly reached by the fires, though similar thickets outside, with longer grass up against them, are raked, and flies in country traversed by these fires continue to survive in small numbers in the hard-pan, and doubtless utilise the hard-pan thickets to the full. Clearing of the hard-pan thickets has a highly marked and immediate adverse influence on the flies.

When I first started work in Shinyanga, the *Commiphora Fischeri* and equivalent wooding was dotted with small thickets. Fly was abundant everywhere and numerous puparia and live pupae were found everywhere in these thickets, at any rate in the dry season. A few years of organised grass burning destroyed a large proportion of these thickets but left relatively intact any thickets protected from high flames by the short, sparse grass of the cemented hard-pan of the drainage valleys. At the same time the fly numbers decreased. When relatively few flies were left, as at one time in Block 5A, it was difficult to find them away from such valleys, even in the thickets that elsewhere survived. The valleys continued to provide a refuge and a combination of rest-haunt, feeding-ground, and breeding-ground, as has been stated above.

7.—THE EFFECT OF CEASING TO BURN THE GRASS AND OF SO PROMOTING THE ADVANCEMENT OF THE VEGETATIONAL SUCCESSION.

It will have been seen under heading 2, "the vegetational habitat" (p. 88 above), that beyond the point at which silt fills up the basins and makes the mbugas, what amounts broadly to a reversal of the natural succession is being brought about, and this is continued by a destructive and deteriorative process which is activated by erosion, accelerated by human activities; the last stage being hard-pan or bedrock. The land now being unusable, the natives evacuate it and (if, by good fortune, tsetses are present) a return on the part of the vegetation towards the climax commences. But if flies are absent, the cattle

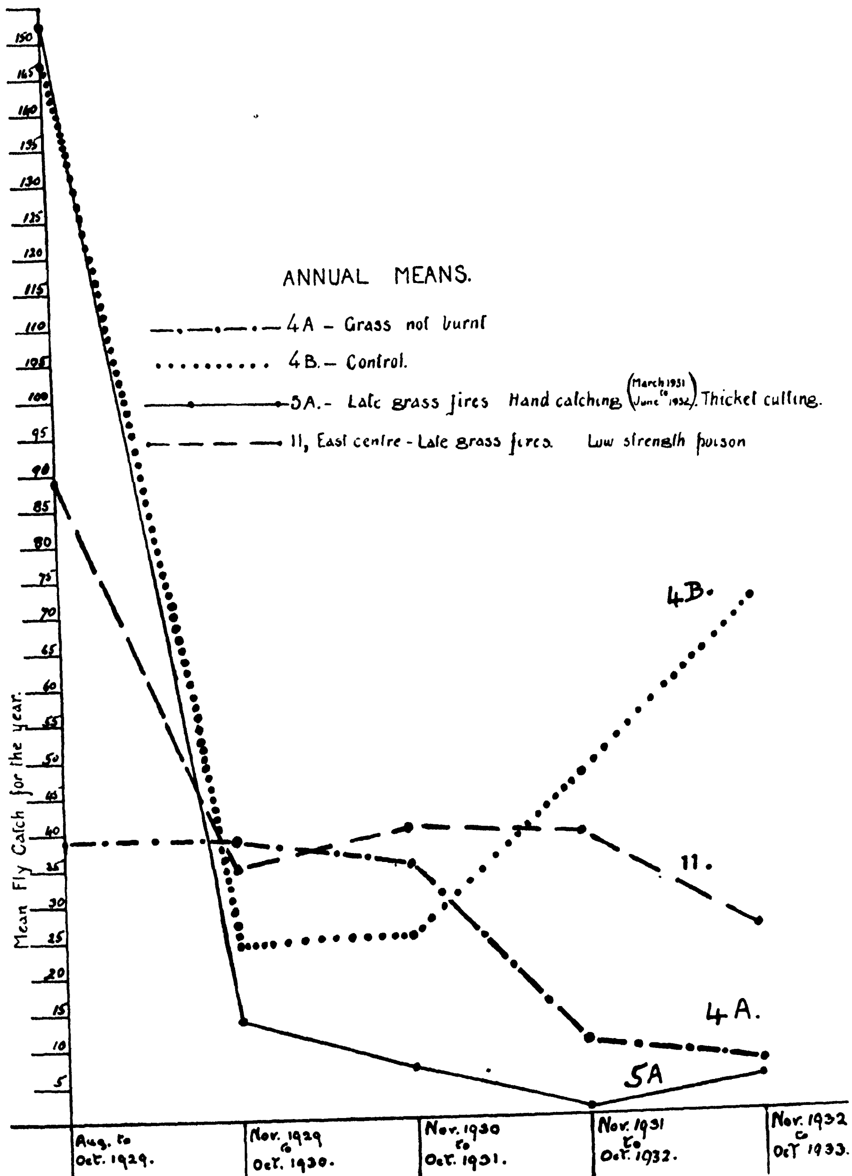


FIG. 10.—The annual means in fly density in four blocks of country infested with *G. swynnertoni* in Shinyanga from August 1929 to October 1933. The three great falls in 1929 followed heavy grass burning late in the season; 4B (subsequent control) was thereafter each year burned early in native fashion and the fly numbers soared; 5A showed a continued reduction to a very low figure during a period of hand-catching off screens in the flies' concentration grounds; 4A was kept unburned altogether and the fly numbers dropped very low; 11 was treated with fires which were only effective on its east and a portion of the fly round was defoliated by means of low-strength arsenical poisoning of its trees. (See fig. 20.)

and goats are shortly turned in again and destroy the beginnings of recovery. This actually was done in Block 9 in Shinyanga in 1934, despite the tsetses (*see* p. 291 below).

On the other hand, with settlement nearly absent and grass fires prevented, more or less dense thicket will tend to cover continuously the ground on the eluvial soil and also the alluvial at most of the stages indicated under heading 2 on pp. 87–89 above, if a live root-supply be in the ground or an appropriate seed-supply be at hand. Progress is much more rapid than in the case of the miombo. Our experiments (pp. 272–275 below) are showing, as might be expected, that *Abrus* and *Markhamia* will be amongst the chief thicket dominants on the eluvial ground, and *Dichrostachys* and *Ormocarpum* on the alluvium, the hard-pan margins, and the less well-drained parts of the granite eluvial.

This difference between the two thicket communities will for long remain marked, but may become less so with the building up of a good bed of humus on the alluvium. It is very probable also that the humus, and the generally improved and equalised soil moisture that may be expected, will bring down from their refuge from the fires in the crannies of the granite kopjes the finer trees, such as the handsome *Commiphora Eminii* and the valuable timber trees *Maba abyssinica* and *Afzelia quanzensis* (the latter already well scattered and reproducing where fires allow), and may spread them through the thicketed land. It is even possible, therefore, that the ultimate climax will deserve a better name than that of "deciduous scrub" (Phillips) which, on present indications, we apply to it.

The effect of the prevention of grass burning on *G. swynnertoni* itself and the probable limitations of this measure are dealt with in Part 3, B, 5 (pp. 272–275 below). It should be noted that continuous thicket—or conditions ubiquitously brought about which are equivalent to thicket—are very different from the broken and scattered thicket (pl. 5, fig. 3; and figs. 5 & 6) that is so favourable to this fly.

8.—THE MATING ORGANISATION OF *G. SWYNNERTONI*.

Like *G. morsitans*, *G. swynnertoni* males wait on paths and on open spaces, and the females repair there also. Like *G. morsitans* it forms following swarms and includes man in the animals followed. In the case of this species again, the fed males fail to follow the hungry females into the uncomfortably open situations which form the pure feeding-grounds, but as this species feeds also in open, badly-grassed woodlands, the males loiter for the females in these. Whether the males, like the females, use the breeding thickets as a rest-haunt is not known for certain; but it is quite likely that they do. Finally, the habit of concentrating more and more in hard-pan valleys, containing a strong thicket element that accompanies reduction in density, ensures the meeting of the sexes down to almost the very last pair.

9.—THE DISPERSAL OF *G. SWYNNERTONI*.

As in the case of *G. morsitans* the general remarks on the dispersal of tsetse which form Section B of Part 4 (pp. 297–307 below) can mostly be applied to *G. swynnertoni* also.

10.—SUMMARY AS REGARDS *G. SWYNNERTONI.*

G. swynnertoni is, next to *G. longipennis*, the fly of the driest and most open areas and is apparently unable to inhabit the more mesophytic savannas. It breeds normally in thicket, though rocks suit it as well, and the rest-haunt of its females at least would appear to be broken thicket. Except when game is superabundant, it appears to be tied to country in some plant community in which thicket figures. It utilises open spaces as feeding-grounds; and the open, short-grassed spaces with very open tree-growth, to which iron oxide crusts and " cement " hard-pans under the soil surface give rise so commonly in its dry thorn-bush habitat, provide it with further feeding-grounds. These, if thickets and trees are present, are used also by the fed population, becoming "hotels," not, like roads and open spaces, mere "restaurants." Its seasonal movements may prove to be both intricate and interesting; for our observations suggest that while it tends to evacuate thicketless country in the dry season, just as *G. morsitans* evacuates country the shade conditions of which become insufficient, it has wet-season movements as well from one plant community to another.

Of the plant communities the most important is that of the hard-pan. Given sufficient thicket scattered through it, the flies can subsist there through the year, and have done so, and in this way incidentally ensured the meeting of the sexes, where our measures—whether hand-catching, burning, or non-burning—have reduced their population to a very low density indeed. The hard-pans, at Shinyanga at least, have appeared to be this fly's heel of Achilles, but for rapid results they must be specially thickened or cleared or temporarily kept clear of food, where such measures are not too expensive. Observations, however, have been made that suggest that the elimination of breeding-sites in particular centres only may also be a blow at this fly. *G. swynnertoni* enters traps even less than does *G. morsitans.*

As regards food animals, this fly is, in the thorn-bush, what *G. morsitans* is in the miombo—primarily and essentially a " game " fly.

11.—THE ECONOMIC IMPORTANCE OF *G. SWYNNERTONI* AS DEDUCED FROM OBSERVATIONS IN TANGANYIKA AND FROM ITS DISTRIBUTION.

G. swynnertoni is as virulent a carrier of nagana in cattle and Rhodesian sleeping sickness in man as is *G. morsitans.* The outbreaks of the latter disease in Maswa, Musoma, and Mkalama have been due entirely to this species. It is almost confined to the northern half of Tanganyika, but it has latterly invaded Kenya fairly deeply between Natron and Lake Victoria and is capable of occupying a great deal of country in that Territory. In Tanganyika it assumes a special importance, being both a vigorous invader of new country and the chief tsetse in the populated, progressive, Lake Province, the natives of which, with their large numbers of cattle, are anxious to reclaim more and more grazing. Much country has actually been reclaimed there, by the making of corridors to open spaces previously inaccessible, by the separation of wooding incapable of permanently carrying this fly from the wooding that kept it infested, and by cutting off blocks of wooding with tribal labour and subsequent attack on them by our measures. Further, *swynnertoni*-country is on the whole more amenable to attack by the promotion of the vegetational succession by not burning the grass than any other of our plant communities—though the hard-pan, where present, must be specially dealt with if it is not to cause delay.

G.—THE RELATION OF *GLOSSINA PALLIDIPES* AUSTEN TO ITS INANIMATE ENVIRONMENT.

1.—THE VEGETATIONAL TYPES WHICH *G. PALLIDIPES* CANNOT INHABIT.

Apparently there are no types of country within its elevational limits that are repugnant to *G. pallidipes*, short of the "desert shrub" land of Shantz, treeless grassland,* or the depths of rain forest, provided that there be present good thicket.† From its thickets as a base *G. pallidipes* will search most forms of country. Moggridge in fact has recently written from Italian Somaliland of "an extremely interesting dry-season penetration of *G. pallidipes* from the Uebi Scebeli (Webbe Shibeli) into and all over a large agricultural area almost devoid of natural vegetation." The flies appear to be guided through this by the scrub which lines the irrigation canals. The Muheza country inland from Tanga offers a similar but perhaps less extreme instance, which is described on p. 176 below.

There are large areas of comparatively thicketless miombo, *e.g.* in western Tanganyika and Southern Rhodesia, that are free from *G. pallidipes.* The more suitable parts of these could probably be invaded if the fly were to come into contact with them. In some cases the necessary thicket connections are lacking for an invasion; in others, such as the great western miombo *morsitans*-belt, invasion is probably progressing south steadily.

To summarise: country without much thicket, especially good riverine thicket, cannot be used by *G. pallidipes*, unless good bases exist close by.

2.—THE VEGETATIONAL HABITAT OF *G. PALLIDIPES.*

G. pallidipes is found in east Africa in a great part of the country inhabited by each of the following flies:—*G. longipennis*, *G. swynnertoni*, *G. morsitans*, *G. austeni*, and *G. brevipalpis.* That is to say, it occurs within every general type of bush country from the drier nyika ‡ to light forms of rain forest (at Kwale near Mombasa and in Portuguese East Africa) and the margins of true rain forest (also in Portuguese East Africa and in small numbers at least in the Usambaras). But all its occurrences have one feature in common; frequent thicket, deciduous, semi-evergreen or evergreen, riverine or other, in clumps or strips, or brokenly covering large areas (as between Dar-es-Salaam and Morogoro), must somewhere in the region be present as a general headquarters and a refuge in time of drought. When the thicket is really dense and continuous *G. pallidipes* seems likely to frequent mainly its outskirts.§ In the actual Juba and Webbe Shibeli valleys, which form its headquarters in dry Italian Somaliland, the humidity, Moggridge reports, is high, though the general climate is desert-like.

3.—THE USE MADE BY *G. PALLIDIPES* OF THE SEVERAL PLANT COMMUNITIES WHICH MAKE UP ITS VEGETATIONAL HABITAT.

(a) General.

G. pallidipes, no less than *G. morsitans* and *G. swynnertoni*, makes use of the concurrences of diverse vegetational types. This statement is based on the observations made so far by all those who have worked on the species in Shinyanga (Potts, Jackson, Lloyd, Moggridge and myself); by Burtt in Mpapwa and Handeni; by Moggridge in Kahama, the Tanga Province,

* See pl. 2. † See pl. 4, and pl. 5, fig. 3.
‡ See pl. 5, fig. 4. § See pl. 6.

and Kwale and Kilifi in Kenya; and by myself in Portuguese East Africa, for over two years in Kilosa, during a number of days with R. H. T. P. Harris and Mrs. Harris in Zululand in the early part of the useful joint work done by them on this fly, and brief or individual observations during fifteen years in various parts of Tanganyika and slightly in Kenya.

(b) The rest-haunt and breeding-grounds.

This fly is based, as stated above, on thicket edges, riverine thicket especially in the dry season, and may even penetrate fairly deeply into extensive and heavily overshaded evergreen thicket (as the semi-rain-forest at Kwale just behind Mombasa in October and certain dense woods on the Sitatonga hill slopes in Portuguese East Africa in July). In the extensive, semi-evergreen, but obviously secondary coastal thicket at Kilifi, dominated in part by *Grewia* and a large *Phyllanthus*, from 20–24 feet high and dense (denser inside than the Kwali semi-rain-forest but not, like it, overshaded), Moggridge so far is taking his captures, which are numerous, on and just behind the margins and roads and not deep inside the thicket.

When I was in Zululand visiting Harris, we found puparia in numbers in thicket in river valleys, in rock-outcrop thickets on the sides of hills, in isolated and "umbrella" thickets, and even in a bed of a low half-shrub *Justicia* (scarcely more than herbaceous), and under a minute, spreading *Grewia* tuft not more than a foot high in grass. The puparia were found almost anywhere under a dry leaf carpet in the thicket, though specially under low overleaning cover, and once (as Harris has recorded, 1930*a* : 40) in the grassy junction of the thicket leaf-layer with the grass country outside, under high shade. We were singularly unfortunate in our searches under rocks, and even a cave between boulders, with soil conditions good, overhung shadily by a small *Schotia* tree and inhabited by a wart-hog, failed to yield anything. The larger thickets referred to, on the rivers, showed many male flies and were therefore probably rest-haunts for both sexes, as the smaller thickets were for the females at least.

(c) The feeding-grounds.

G. pallidipes freely scours for food the open savanna wooding in leaf, the edges at least of mbugas and glades, and roads through thicket and otherwise. This is deduced from the captures of many thousands of hungry flies by traps, on screens and by hand. Moggridge took flies on the road running through the Kilifi thicket on the Kenya coast at the rate of 30 an hour, which showed a mean hunger stage of 3·33, with a ♀ percentage of 55. At the contact of thicket with old cultivation the figures were 11 per hour, M.H.S. 3·60, ♀ % 57. At a contact with present cultivation the figures were 14, 3·5 and 50.

In Mpapwa the breaks in the riverine forest that contained water-holes used by cattle were the sites of the feeding concentrations of this species in the dry season.

The reactions of feeding *G. pallidipes* to trapping in the local vegetational types and combinations are described on pp. 256–258 below. The conclusion there stated that heavy thicket was unfavourable does not imply that heavy thicket is not used by the fly. It was merely unfavourable to *feeding* flies—which are those that come to the traps. *G. morsitans* females also within their breeding-places are far less ready to appear than in their feeding-grounds, and in the case of *G. pallidipes* the males also do not come readily to man. Actually proximity to the enthicketed dry stream, regarded as the retreat of

the fly, seemed to give a tendency towards success. Glades, open spaces in and beside thicket, and light thicket, all more or less serving as feeding-grounds, were also more or less favourable, while open mbuga gave medium success. The fact that distant visibility appeared to exert little influence, while proximity to the thicket margins was favourable, was rather paralleled in the case of *G. palpalis* by the differential results obtained by the Chorley traps, and suggested that the flies searched closely along these margins—a conclusion that would fit the views both of Fiske (1920) and of Harris.

(d) Instances of the miniature, but successful, concurrence of all the elements needed.

Harris regarded a thicket, which might be quite small, a game-path, and a water-pool or wallow, as being a combination which commonly yielded *G. pallidipes* and its pupae, and he showed me some such spots. Here apparently were what we should call breeding-ground, rest-haunt, and feeding-ground, all concentrated in the smallest possible space.

A particularly interesting and isolated *pallidipes*-belt in very small miniature was discovered at Dar-es-Salaam in October 1934. The fact that cattle grazing in the coconut palms in the northern edge of the town were developing trypanosomiasis attracted attention, and a search was made by Dr. W. J. Aitkin, Acting Senior Medical Officer of Health, and by Capt. M. A. Molloy, the District Veterinary Officer, the latter employing fly boys from Mpapwa. A focus of *G. pallidipes* was found in a limited piece of thicket within the township, only a few hundred yards long and averaging perhaps nine feet in height. It ran along the top of the high, curving bank of a broad mangrove creek which, with much native cultivation beyond, separated the focus from the nearest extensive thicket that might have sheltered the species. Flies were captured at the quite high rate for this species of 16 and 18 an hour. The concurrence of the vegetation communities was perfect for this tsetse. There was the thicket to take refuge and breed in, and between it and the town was a coconut plantation with short, grazed grass, that, with cattle wandering through it, formed a good feeding-ground. I searched the thicket for animals and found spoor that indicated the presence of one (or possibly two) pairs of Harvey's duiker. It is very usual, however, for monitor lizards to inhabit thicket of this type abutting on mangroves and to feed on the crabs in the latter. Time was too short to test the possibility, which exists, that the *G. pallidipes* present may, like *G. palpalis*, have been feeding on lizards and using the mangroves as a feeding-ground.

The turning over to cultivation of this Bagamoyo-street colony of *G. pallidipes* has been a simple matter, with a market for produce on the spot.

4.—THE PHYSICAL FACTORS.

(a) The geological and elevational habitats as indicators of physical factors.

As there is no savanna type in which *G. pallidipes* may not appear, provided that good thicket is somewhere present, there can be hardly a geological type which will not support it. The species occurs up to 6,000 feet in the Mbulu District, at sea-level on the Equator, and not much above it in Zululand, 28 degrees away. Its upward limit in Zululand is 1,500 feet, but, as Harris (1930*a* : 8) points out, this represents the elevation at which bush tends to give way to grass country in any case.

(b) The standard climates of *G. pallidipes.*

At one extreme *G. pallidipes* enjoys, in high density, the hot, moist climate of the equatorial coasts of Kenya and Tanganyika, which need not be described in more detail. At the other extreme it supports, in equal density, a climate which drops to freezing-point. Harris (1930*a* : 10) wrote as follows of the climate of the belts of *pallidipes* in Zululand :—

"The summer temperature before and after rainfall in December and January rises at times during the day to a maximum of 112° F. in the shade, falling at night to between 85° F. and 90° F. In the winter months the temperature shows greater variation. It seldom rises above 80° F. in the day and falls at night on rare occasions to 32° F. The average minimum temperature in mid-winter at night is in the region of 50° F." The average rainfall is under 30 inches or approximately that of Shinyanga, but the country is subject to serious failures of the rains and an occasional deluge.

No *G. pallidipes* existed at Kikore during our investigation there, although the species might well have done so and one or two immigrant individuals have been taken since. The types of vegetation there studied are used by this fly elsewhere as feeding-grounds, and the results of our study of the physical conditions in these are given on pp. 66–68 above. At Shinyanga *G. pallidipes* is present as a small population averaging about four per screen per 10,000 yards. The standard climate of the locality is described on pp. 64–66 above. That of the lower margins of the rain forests of the Usambaras, on which margins *G. pallidipes* occurs, is given under *G. austeni.*

(c) The eco-climates of *G. pallidipes* at Shinyanga.

The readings of the atmometer in the riverine thicket, given on p. 98 above, are descriptive of the range in the evaporative power of the air through the months in the rest-haunts of *G. pallidipes* in Shinyanga; the others are indicative of the conditions in the parts of the Shinyanga country that it scours for food and in which (pp. 251–258 below) it comes to our screens and traps. Moreau's observations on the eco-climate of the Lowland Forest near Zigi on pp. 165–167 below, apply, as regards its margins and breaks in it, to this species also.

(d) The round of the seasons, and its effect on *G. pallidipes.*

G. pallidipes is taken by hand in such small numbers during most of the year in Shinyanga that it has seemed hardly worth while there to attempt to work out its full seasonal relationships. It is, however, the case that in the late dry season there is comparatively a burst of these flies coming to man, and a smaller one in the short dry season in February; further, on the Ngongho stream our traps, in September particularly, have caught quite large numbers of these flies.* During the rest of the year, and especially during the wet season, traps (both ours and the Harris trap) have been ineffective. This is obviously a hunger effect. As regards appearance to man, females of *G. pallidipes* become hungry under dry conditions like other flies of the *morsitans* group, but unlike their males, do not normally appear to the catchers in any large numbers when not hungry.

As regards the hours of activity—an indication also of relative tolerance of dryness and heat—*G. pallidipes* comes to our traps in very low numbers, if at all, once the day becomes hot and in really large numbers only after 3 or 4 p.m.

* See p. 257.

(e) Cases of sparse but effective occupation of country by *G. pallidipes*.

The case of Mpapwa is dealt with under "surveys" on p. 340 below. To quote further from my letter of 9.xi.1932 to the Director of Veterinary Services, we have the following analogous cases:—

(1) In Zululand *G. pallidipes* was established in the Ntambanana Settlement. No flies were ever seen in the latter, yet in some seasons odd cases, in others big outbreaks, of trypanosomiasis occurred here and there in the cattle on the farms. Eventually it took a very prolonged and patient investigation by Bedford, using bait-cattle and horses, to unearth two flies here, five there, one somewhere else, and so on, proving that a light infestation (or light visitations) occurred in the settled area. Two of these flies were taken in the valley just under the Veterinary Research Station—yet previous to this flies had never been seen there.

(2) Outside the border of the Melsetter District of Southern Rhodesia, in Portuguese East Africa, there runs a *pallidipes*-belt, already known to exist in its present position in 1897 or earlier. No flies were ever seen on the Rhodesian side of the border till two or three years ago (when one fly was taken), despite painstaking searches by myself and others and a careful look-out by thoroughly intelligent farmers. Yet, right along, in some seasons odd cases, in others more definite outbreaks, have occurred on a number of the border farms. Very gradually the situation has become worse; losses have tended to occur more in the heart of the district near wooded valleys of rivers that pass out through the border, and heavier outbreaks have occurred on the latter; yet such cases may have been followed by one or two years of immunity. About two farms only, on the border, had become untenable by cattle, and this was apparently through the increased upgrowth of thicket which resulted from the reduction of grass burning. The one fly taken was many miles inside the district.

(3) The difference between these cases and that of Mpapwa is that the country of the sporadic outbreaks in Zululand and Melsetter is on the whole, except for its river valleys, much less suited to the presence of *G. pallidipes* than Tubugwe and Kikombo appear to be. This makes it strange that these latter places have not long become permanently infested; and the danger remains that, with any heavy increase of fly in Ntambi and consequent reinforcement of hungry wanderers, this may yet occur. In any case, comparing these places with the two lost border farms in Melsetter, such losses may yet occur in some years from sporadic invasion in numbers sufficient to make the situation impossible.

(f) Evacuation of country, and concentration on the part of *G. pallidipes*, as the result of excessive drought and (probably) excessive humidity.

In Mossurise, in Portuguese East Africa, I noted active concentration taking place on the part of this fly, accompanied by evacuation of country, at river-thickets and on the edges of mbugas with some thicket, which were concentration sites for *G. morsitans* in July. Re-dispersal through the general savanna was recorded as beginning in November. Burtt, reporting on the very dry country of north-west Handeni in September, writes of *G. pallidipes* that "it is apparently confined to shady stream-beds during the severe dry-season conditions and later with the flush of leaf in the 'pori' (bush) becomes distributed over wide areas by its own propensity for wandering and possibly by the movements of game."

Harris (1930*a*) wrote of Zululand that " in the winter months the flies become scarcer and appear to concentrate in valley bottoms and other parts where evergreen trees are the rule " (p. 34); and (p. 36) " my experience is that during the winter months flies are practically absent from the deciduous bush where the leaves have fallen. . . . In the summer months when the trees are all in leaf, flies may be found almost everywhere in the bush country." F. Vaughan-Kirby, Game Warden in Zululand, told me that in the winter (dry season) one could even ride right through the leafless savanna thorn-bush of the Umfolozi Reserve (at other times infested) without having one's horse bitten.

Burtt also—and this is exceedingly interesting in view of the observations quoted already as to wet-season evacuation of thicket and the richer savanna by *G. swynnertoni*—in the course of wet-season and dry-season investigations near Mpapwa concluded that wet-season evacuation took place also of riverine strips showing luxuriant grass-jungle conditions, although these strips appeared essential to the fly's existence in the dry season. The movement was to " dry " thicket. A fuller account of this important investigation and its conclusions is given on pp. 340–345 below.

Further cases of selection, possibly seasonal, between thicket types have been noted. At Kwale, Moggridge found this tsetse still apparently confined to some (not all) of the major semi-rain-forest patches (with very dense vegetation) in December, flies being caught at the rate of 14 per hour, all completely without hunger. They spread thence, he believes, into small outlying clumps dotting the country and into narrow riverine thicket during the rains, but it has yet to be ascertained whether they at the same time evacuate the rain-forest patches. He did not think that the movement of buffalo herds in and out of the locality, which took place, had much effect on the average fly position. He found also that in Nindo (West Shinyanga) the more heavily-thicketed areas were least productive of *G. pallidipes* even at the end of July. Wallace found few about the outskirts of the heavy rain forest below Amani and none inside it in May 1926, with a high temperature and a daily deluge of rain during the first week of the work and light rains with cool weather afterwards. I found in Mossurise in the middle dry season that not all types of thicket were equally suited to *G. pallidipes*, relatively low thicket, as opposed to high dense forest and to thicket continuously shaded with canopy of any kind, being indicated as its preference there in June and July.

Harris (1930*a* : 74) records that the periodic dispersal of tsetses in search of game which in times of drought moved from the Reserve to the " buffer strip " made the latter area in Zululand much more a resting and breeding-place of the flies than in times when the game had retreated. Actually the buffer area as shown to me had also a game population of its own, but any desertion of the Reserve hard by would no doubt have the effect described.

From all the above it is concluded that not only is clearing, separation, or mere modification of one essential community all that is needed anywhere to eliminate *G. pallidipes*, but that not every part of that one vegetational community is of equal importance, or is important, all the year round. Discriminative clearing, and further clearing, well watched, through bush connections to cut off seasonally infested wooding from permanently infested wooding, are thus indicated as worth testing in the future, but fuller investigation is regarded as desirable meantime and will be undertaken by Moggridge.

TABLE 10.

Times of day when captures of G. *pallidipes* were made in the dry and rainy seasons respectively, in Mpapwa District, Tanganyika Territory, during Burtt's survey in 1933.

Time	Dry season: no. of flies	Rainy season: no. of flies	Time	Dry season: no. of flies	Rainy season: no. of flies
6 a.m.	1	—	1.30	—	3
6.30	—	—	2.00	—	7
7.00	—	—	2.30	—	31
7.30	—	—	3.00	—	3
8.00	10	—	3.30	—	1
8.30	3	3	4.00	—	20
9.00	9	15	4.30	—	1
9.30	3	40	5.00	2	—
10.00	6	76	5.30	11	—
10.30	1	34	6.00	18	14
11.00	4	19	6.30	15	30
11.30	6	1	7.00	1	19
12.00 noon	6	5	7.30	—	1
12.30 p.m.	1	1			
1.00	2	—			

5.—THE EFFECT ON *G. PALLIDIPES* OF GRASS FIRES.

(a) The effect of the ordinary annual grass fires.

In Shinyanga no evidence has been obtained which shows that the relation of *G. pallidipes* to the ordinary annual grass fires is different from that of *G. swynnertoni*. For both, it ushers in a hard, intensely dry period, and *G. pallidipes* in the time intervening between the fires and the rains is forced to appear to man and especially to screens and to traps in far larger numbers than at any other part of the year. The flies that come are all hungry. At the same time during the period of years in which intensive grass burning has been employed in certain blocks, the general infestation of *G. pallidipes* in Shinyanga has increased.

(b) The effect of organised fires late in the season.

The effect of our organised grass fires late in the season is also the same as it is on *G. swynnertoni*. When the last-named fly has been locally driven out by them, *G. pallidipes* has not remained. Generally the effect of fires late in the season is to burn out more of the thickets each year and thus to limit one of the vegetational necessities of this tsetse more and more to the valley bottoms and hard-pan which do not burn out so readily and which, with organised grass firing combined with discriminative clearing, is all that needs to be modified.

6.—THE EFFECT ON *G. PALLIDIPES* OF ADVANCING THE VEGETATIONAL SUCCESSION BY NOT BURNING THE GRASS.

The effect on *G. pallidipes* of advancing the vegetational succession by not burning the grass is dealt with on p. 277 below. We do not know how this method will affect *G. pallidipes*, and experiments for testing it are very urgently needed, in case non-effect on *G. pallidipes* may prejudice our work on these lines against *G. swynnertoni* and *G. morsitans*.

7.—THE MATING ORGANISATION OF *G. PALLIDIPES.*

While there are localities in which this fly is dense, it can and does occur over most of its vast local range as a sparse population—often very sparse indeed, yet capable of excluding cattle or causing great losses thereof, as it did in Ntambanana in Zululand, on the Chipinga–Portuguese border in Southern Rhodesia, and in Mpapwa in Tanganyika Territory. In this it differs completely from the other common species of tsetse, which essentially live in strong colonies. But that individuals are able to collect together and the sexes to meet where the population is sparse is indicated by repeated observations in Mossurise, where attacks of this fly were experienced at points some miles apart in continuous similar wooding, although not a single fly was seen in the intervening areas.

8.—THE DISPERSAL OF *G. PALLIDIPES.*

Individually *G. pallidipes* gives the impression of being a bold independent rover to a far greater extent than do the other species of tsetse. Thus one expects it in dull weather to cross clearings that other tsetses would not. The apparent initial result of the Southern Rhodesian Government's clearings across river valleys leading into the infested area in Portuguese East Africa has, however, not borne out this expectation, although it is too early to feel sure, nor has the apparent initial result of the clearings undertaken in 1933 near Mpapwa. Certain farms in Zululand carried strips of bush connected with the fly belt proper, and where these had been cut across by a clearing no tsetse could be found on the farms when searched for by T. C. Cairns; but farms not similarly treated remained infested. Harris's special experiments, on the other hand, bear out the expectation very thoroughly, for they demonstrate the regular passage of flies of this species, not only to a small patch of bush surrounded by a clearing 400 yards wide at the narrowest which game animals were prevented from entering, but also across a space more than 1,000 yards wide, consisting partly of grass and partly of a great white sandy stretch of sheer river-bed, with a bush-clad cliff conspicuously visible on either side. That such clearings may act as a strong check, by reducing the wanderings of the flies except in certain types of weather, is however more than likely.

Curson notes that "following flies" of this species leave when open country is reached. Harris records that a following swarm leaves bait-animals when this happens, but that hungry flies, intent on feeding, go on. The parallel with *G. palpalis* is here exact. Persistence of the flies up to 900 yards into open country was observed by Cairns, at that time Harris's assistant. Everyone who has seen much of this fly regards it as a bold and far wanderer when hungry. Also it will break away from the main population and live sparsely.

In general, therefore, it may be said that the powers of dispersal possessed by this tsetse are probably particularly strong. Harris, like Fiske in the case of *G. palpalis*, concluded from his observations that, if concentrations of game animals are rare, the flies may wander further and further into areas unsuitable for breeding and disappear.

9.—SUMMARY AS REGARDS *G. PALLIDIPES.*

G. pallidipes is capable of infesting any of the Tanganyika tree savannas, mesophytic or dry, provided that thicket systems or thicketed streams (seasonal or flowing) are present that it can use as its base. It is a thicket-

breeder and its rest-haunt is thicket also. It feeds in the open savannas and investigates glades, water-pans, hard-pan strips, the edges of plains, and other feeding- and drinking-grounds of the game, probably, as Harris concluded and as our trap results also suggest, following definite routes through the bush.

Its seasonal movements, like those of *G. swynnertoni*, comprise in some areas (at Mpapwa) not merely an evacuation of the drier of the elements of its habitat in the late dry season in order to concentrate near the streams, but also an exchange in the heavier rains of the heavy-thicket types used in the dry season for the " dry " types of thicket on well-drained ground, which it avoids in the dry season. It is possible, therefore, that two thicket types are necessary to its survival in a locality. Placing cleared barriers across the routes of its seasonal movements along valleys seems to have been effective initially both in Mpapwa * and in Southern Rhodesia; and amongst measures that will be worth testing are elimination, modification, or segregation of one thicket type only which in a locality has proved to be necessary to this fly in one season only of the year.

When hungry and also abundant, *G. pallidipes* can be caught in very large numbers in traps, whether ours or those of Harris, but our effective trapping, with either type, has been confined to the late dry season. In Zululand the effective period appears to have been much longer. Certainly, under the conditions in Tanganyika, sparse *G. pallidipes*, covering vast areas of country, cannot be exterminated by traps.

As regards food animals, *G. pallidipes* in its ordinary surroundings is as much of a general game fly as is *G. morsitans*. But hiding itself inside thicket and living as it does also in country covered with at least broken thicket, it becomes probably to a special extent also a feeder on buffalo, bush-pig, bushbuck, Harvey's duiker and suni. In the country investigated in Mpapwa its dry-season feeding-concentrations were almost confined to the water-holes used by cattle, but its habit of avoiding the hot hours, and the formation by the cattle-owners of the habit of watering their beasts at midday, was averting rapid destruction of the herds.

10.—THE ECONOMIC IMPORTANCE OF *G. PALLIDIPES* AS DEDUCED FROM OBSERVATIONS IN TANGANYIKA AND FROM ITS DISTRIBUTION.

G. pallidipes carries freely the parasite of nagana and is effective in excluding stock from the country it infests. It does not feed nearly so readily on man as *G. morsitans*, *G. swynnertoni* and *G. palpalis*, and in this way its danger as a vector of human trypanosomiasis is enormously reduced. At the same time Corson found that it becomes infected with trypanosomes of the *brucei* (human) group with (apparently) special facility. It will be noted that, given adequate and suitable thicket, *G. pallidipes* may be found in most types of country and up to an elevation of 6,000 feet. The number of degrees of latitude covered by its distribution, also, as might be expected, exceeds on the east coast those infested by any other tsetse. It ranges from the Webbe Shibeli in Italian Somaliland down to Zululand, with the exception of certain large areas, some of which appear to be in process of being invaded. It extends westward to the full depth of Kenya and Uganda, Tanganyika and Portuguese East Africa, and into the Katanga Province in the Belgian Congo, with again large omissions, but has been recorded little so far beyond till we reach the land of its west African geographical representative, *G. longipalpis*. It is present in the

* See fig. 23.

Anglo-Egyptian Sudan (Nerusi, west of Mt. Zulia) and in Nyasaland in the Shire Highlands and (probably) on the Lunyina river.

A disconcerting result of the fact that *G. pallidipes* appears infrequently to man is that it may infest a country lightly and cause great annual losses of cattle, without ever being seen. Zululand, the border farms of the Melsetter district in Southern Rhodesia, and Mpapwa in Tanganyika, have all afforded good instances of this. In each case, direct transmission without more than the rare aid of the tsetse was suspected in consequence of the losses, but thorough and prolonged search in Zululand and Mpapwa in each case revealed the presence of *G. pallidipes*. In Melsetter, despite many thorough searches (some by the Rhodesian Government Entomologists, some by myself) and a look-out by intelligent and educated farmers and missionaries over a period of quite 15 years, not a single example of *G. pallidipes* was seen, though it was known to occur in numbers just over the border. At long last, however, one or two have been found in the district. In Kenya, similarly, outbreaks and cases of animal trypanosomiasis have occurred in a number of places in which tsetses have never been seen (Lewis, 1934).

Finally, as will be seen on p. 171 below, *G. pallidipes* may possibly threaten the success of our most promising measures against *G. morsitans* and *G. swynnertoni*.

No fly in east Africa exceeds *G. pallidipes* in importance in relation to animal trypanosomiasis; *G. morsitans* probably equals it.

H.—THE RELATION OF *GLOSSINA AUSTENI* NEWSTEAD TO ITS INANIMATE ENVIRONMENT.

1.—THE VEGETATIONAL TYPES WHICH *G. AUSTENI* CANNOT INHABIT.

Extensive and unbroken true rain forest, savanna wooding where it is cut off from thicket, and open country appear to be the types the interior of which *G. austeni* will not inhabit.

2.—THE VEGETATIONAL HABITAT OF *G. AUSTENI*.

The type locality, Jubaland, " is apparently all alluvial soil, chiefly the extremely fertile black cotton soil. There are occasional swamps or deshehs which are filled up by the floods in November or October and are dry for the most part by the following June. The river banks and the edges of the deshehs are covered with forest," including palms, figs and euphorbias—and therefore what here we should call secondary (Filleul, quoted by Newstead, 1924).

Our own finds of *G. austeni* have been both on alluvial and eluvial soils and have occurred anywhere between the coast and the central plateau, but not on or west of the latter. Wallace's investigation, to be described later, revealed large numbers of *G. austeni* on steep mountain slopes.

In the case of the extensive coast habitat of *G. austeni*, *G. pallidipes* and *G. brevipalpis*, near Kilifi in Kenya, Moggridge has found that along the coast there is a belt of extremely dense thicket apparently more or less evergreen, and that, further inland, there is similar thicket broken up into patches by channels of open grass country. He is taking specimens in the coastal thicket where it adjoins cultivation and roads but not deep in the thicket; and also deep in the broken thickets. Wallace took most of his specimens on and in the outskirts of secondary rain forest with savanna elements intermingled and in thicketed tree plantations. I took my specimens in secondary forest and thicket. Much detail is included under headings 3 and 4 below, in view of the

fact that so little has been recorded on this fly hitherto. Meantime it may be said that *G. austeni* (like *G. pallidipes*, *G. swynnertoni*, *G. palpalis* and *G. brevipalpis*) appears always to be based on thicket, but on thicket of secondary type rather than on continuous true rain forest, or continuous primary type thicket, though it may use the margins of these, or be attracted to concentrations of mammals a little way in.

3.—A MOUNTAIN HABITAT OF *G. AUSTENI*.

(pl. 6.)

(a) Description of the investigation.

In May 1926, G. B. Wallace, then our microbiologist, investigated the distribution of *G. austeni* in the Zigi valley immediately below Amani, and the surrounding slopes of the east Usambara mountains, the area having an elevation from 600 to 3,000 feet. The geological formation consists of gneisses of the basement complex (Teal, 1933); and the soil is a very red and very acid loam, 1–10 feet deep.

The vegetation. Looking north from Hartmann's plantation on a low spur of the eastern Usambaras, across the far-extending steep eastern slopes of Bulwa, and turning to look south-west past Amani, one sees that the top of the range is still mostly covered with evergreen rain forest. Down the Bulwa slopes from this forest run lines and narrow tongues (often following ravines or marking rock-outcrops) of tall trees and dense vegetation which are separated by broad wedges of grass-land. These wedges may be open, but more generally they carry a sparse tree savanna. Glancing east to the isolated mountain, Mlinga, or south-west to Amani, one sees what it is that has produced this effect; for the open slopes in these cases are still covered with the red and light-green patchwork of present cultivation, as is the "plain" of low hills below. All these areas and the mountain slopes were originally unbroken, magnificent, rain forest, but this is being exterminated, except where the government happens to protect it. The first attack is by native cultivation, and where this is abandoned the fallow becomes covered in the main by grasses which dry seasonally. Amongst them spring up the rain-forest pioneers and the fire-standing trees of savanna, which compete with each other. Which wins (and it is usually the latter) is decided by the annual grass fires, still lighted by the natives following on the abandonment of cultivation. These fires, given an extensive run and a fairly severe dry season, extend still further the destruction of the forest.

The result, which is of importance to our problem and is shown generally on pl. 6, is that, in exchange for rain forest only, the ground that was investigated is now, in its relation to the tsetse, carrying fourteen categories of covert, of which however four are provided by the plantations of the Amani Research Institute. All but the fourteenth (unsearched) are described briefly in the table (table 11) given below. The categories (i), (ii), (iii), (iv), (v), (vi), and (xi) of the table are mostly on very steep slopes.

The larger mammals. Bush-pigs (*Potamochoerus koïropotamus daemonis*) were in moderate numbers and well distributed. In particular a large area of the abandoned gardens next to the rubber above Zigi house had been turned up by their rootlings, and tsetse were abundant in this neighbourhood. Monkeys were coast-forest guereza (*Colobus polykomos palliatus*), coastal "blue" monkey (*Cercopithecus leucampyx* prob. *kibonotensis*) and North Tanganyika vervet (*C. aethiops johnstoni*), moderately numerous but all probably quite un-

important. Tree hyrax was present (*Dendrohyrax terricola* and probably *vosseleri*). Of baboons about 30 haunted regularly some secondary forest on the Zigi. A few Harvey's duiker were seen and a few bush-buck were present. The pigs certainly were the main food animal.

During the first week of the investigation the temperature was high and there was daily a protracted deluge of rain. During the later weeks the weather was much colder, but the rainfall diminished very appreciably.

Bait-cattle were used, and of the total of 421 adult *G. austeni* captured only one was taken at man.

(b) Details of Wallace's catch.

The details of Wallace's catch are given in table 11 on p. 116.

(c) Deductions.

From these data the following deductions are made.

Evidence from density. The Ceara rubber, the mixed thicket (iv), the abandoned and burned cultivation, and the teak were by far the best populated of the plant communities searched and were therefore presumably the headquarters, or close to the headquarters, of the local population of flies. The test is probably good, as the bait-cattle were obviously effective in bringing *G. austeni* out.

Evidence from breeding sites. The 261 pupae and pupa-cases were all taken in the mixed thicket (iv) or (a few) in the teak. These two types of cover are therefore attested by two lines of evidence to be the " home " of the flies. The evidence of the finding of pupae was wanting for the rubber plantation and the abandoned cultivation.

Evidence from composition. Even at cattle, the female percentage should not be much higher in the rest-haunt than 50%, and we find this proportion most nearly approached in the mixed thicket and enthicketed rubber (47% and 52%). The teak comes fairly near with a percentage of 58. Despite the presence of rocks and a few pupae it is devoid of undergrowth, and it might therefore be in part a feeding-ground also.

The abandoned cultivation, partly young thicket, partly more open, should be either a mixed feeding-ground, in which replete males mingle with hungry flies of both sexes, or a patchwork of rest-haunts and feeding-grounds. Its female percentage, being 62, would lend itself to either interpretation.

On the analogy of the habits of the other species of tsetse, the remaining places, in each of which few flies were found, should be feeding-grounds rather than rest-haunts and should show a high female percentage. Savanna shows 66% and *Raffia, Cananga, Citrus*, dense secondary rain forest and cultivation, 100% each—numbers being admittedly very low. On these figures by themselves, we might hazard the view that dense secondary rain forest (12 flies) was unfavourable in that it was too dense and the others in that they were too open, but that hungry flies traverse anything and use these areas when searching for food. On the other hand, low numbers attach also to true rain forest (2, female % 0) and *Cedrela* (9, female % 44), the former of which is dense and the latter (one would suppose) not unsuitable to a fly which likes the mixed secondary thicket and the rubber.

Other evidence, such as the fact that only these two examples of *G. austeni* and three of *G. brevipalpis* were taken in a 20-mile search of the rain forest, shows that despite the male sex of the specimens of the former species, rain forest is not favourable. Wallace suggests that they may have

TABLE 11.

The details of Wallace's catch of *G. austeni* in May 1926, below Amani, Tanganyika Territory.

Types searched (i–vi in order of vegetational succession)	*G. austeni* ♂	♀	Total	♀ Percentage	Notes
i. Primary rain forest	2	0	2	0	Tall, with undergrowth dense but traversable, evergreen, cool, light much subdued. Some extensive unbroken stretches, which generally are very uniform. "Intermediate" and "Lowland Forest" of Moreau (*see* p. 121 *et seq.*).
ii. Native cultivation:					On steep slopes whence rain forest has been cleared; scattered trees and banana clumps, fairly uniformly open and insolated, except where crops are high.
Maize	0	2	2	100	
Cassava	0	1	1	100	
iii. Old native cultivation, abandoned and partly burned through	37	62	99	62	Complete interspersion of dense growth and open areas, of low regenerating rain forest and savanna elements, of shrubs and tall grass and weed clumps, with low grass and herb carpet interpolated through burning.
iv. Mixed thicket, young rain forest predominating	43	38	81	47	Succession much further advanced. Dense rain forest and savanna types, the two still struggling for predominance, but the rain forest winning; varying in density and amount of light reaching the ground.
v. Savanna wooding	1	2	3	66	Aided by the fires, savanna has won against rain forest in the struggle of regenerating elements. Very open, trees low. Grass high and low. Sometimes, after omission of burning, invaded from the edges by (iv).
vi. Secondary rain forest, partly regenerated, such as would ultimately again become (i) in general composition and appearance	0	12	12	100	With fires locally excluded, rain forest has won. Uneven in height, but dense below and difficult to traverse where formerly cleared; cool, but slightly less so than (i). Light less generally subdued; occasionally quite extensive. Probably not very dissimilar in ecoclimate from Moreau's "Lowland Forest" (*see* p. 121 *et seq.*).
vii. *Citrus* spp.; tree and shrub plantations	0	1	1	100	Conditions exposed, light and dry. A strip of rain forest on one side, beyond which is again open clearing. Next to the *Cananga* and beside the motor road.
viii. *Coffea robusta* and *C. arabica*	0	0	0	0	Ground fairly shaded by the coffee and in parts by *Grevillea* trees also.
ix. *Cananga odorata* with *Funtumia elastica* and *Castilloa*	0	5	5	100	15 ft. spacing, clean-stemmed up to 30 ft. Canopy thin, much light penetrating to the 1-ft. high grass carpet. Adjoined on one side by the narrow band of rain forest just mentioned, on the other by a mowed grass strip by the Zigi stream. Traversed by a motor road and containing our bait-cattle shed.
x. Raffia palms and bamboo	0	1	1	100	Each plant dense in itself; but the whole openly planted. The one fly was taken in the palms.
xi. Teak (*Tectona grandis*)	19	26	45	58	Dense foliage coming fairly low and shading well the grass-covered, leaf-littered ground, separated from the Zigi river by a narrow belt of bamboo. Elsewhere adjoined by abandoned cultivation. Many rocks.
xii. Toon (*Cedrela odorata*)	5	4	9	44	(*a*) On steep slope to river, fairly lofty, canopy thin and shade poor, grassed underfoot, adjoined by secondary forest. (*b*) Unweeded and with thinnish forest undergrowth. Catch not differentiated as between (*a*) and (*b*) but in the main or entirely from (*b*).
xiii. Ceara Rubber (*Manihot glaziovii*)	77	83	160	52	Rubber trees to 30 ft. high. Between them a close undergrowth of indigenous shrubs and sometimes underplanted *Leucaena glauca*. Ground stratum of shade-bearing grasses and herbs. Very sheltered, and (where most *G. austeni* caught) moderately shady. Elsewhere (most *G. brevipalpis*) heavier shade, about equalling (iv).

been carried into the rain forest on animals, as he has seen happen. And as regards the toon, the proportions were of the type which we are (arbitrarily) taking here to be those of the rest-haunt, and rest-haunt conditions were duly present even if the site was not popular. Wallace gives instances to the

contrary, in which open spots yielded more males, and denser cover alongside more females, but, in any case, the bulk of his flies (in the rubber and the mixed thicket) were taken just within the margins of the wooding and he failed to find many further in. An equivalent to the "male swarm" of other tsetse species on the edge, with the females lying low just inside till the cattle walk right in amongst them, would not be incompatible with what might be found in the haunts of these other species. It is probable enough also that these margins were of "hotel" type, fed males mixing with hungry females and males and swelling the male proportion.

Evidence from condition. No such evidence is available, as we had not then developed our methods of analysing hunger.

Taken generally, the results seem to indicate that the densest types of wooding are inimical, at any rate when highly extensive; that a dense, but not over-dense, cover is the optimum for the rest-haunt; that very open types are inimical, except for feeding flies; that these types and the densest are entered by flies seeking food; and that addiction to vegetational contacts (the edge of the rubber, the edge of the mixed thicket, the abandoned burned native cultivation with its very strong interspersion of open and dense vegetation) is strongly developed in this species.

It would be fully in line with our many observations elsewhere on the habits of this particular fly, if we assumed from the data above that the semi-dense (yet heavily shaded) types, such as the more open rubber, the mixed thicket, and the dense patches in the abandoned cultivation, were more popular than the densest rain forest, whether primary or regenerated secondary.

4.—FURTHER EVIDENCE ON THE USE MADE BY *G. AUSTENI* OF THE SEVERAL ELEMENTS WHICH MAKE UP ITS HABITAT.

(a) General.

Burtt, on 11th February, 1933, in the Kidete valley, on ground cleared originally of forest of more or less gallery type and now regenerating after cultivation, took a very hungry male *G. austeni* on the knee of a bait-ox, natives present being neglected. It was in one of many small open glades which interspersed fairly dense leafy jungle of *Microglossa* and *Sesbania aegyptiaca* under dotted *Acacia campylacantha.*

Swedi bin Abdallah, head fly boy, took quite a number of *G. austeni* with bâit-cattle along a deciduously thicketed ravine, the cover being of climbing *Combretum padoides,* the dense shrub *Acalypha ornata,* and such Commiphoras as *C. Merkeri.* No tree exceeding twenty feet in height was present. Three hundred yards away was tall, denser forest on the river, but in this no *G. austeni* could be found at that season. A ravine of the type concerned would be a dry baked furnace in the late dry season. It may be surmised that *G. austeni* might take refuge then on the river. Odd examples of *G. brevipalpis* were present at the time, both by the ravine and on the river, thus affording confirmation of Wallace's diagnosis of the relative requirements of these species.

The Kilifi coastal thicket, which Moggridge is working, has been briefly described under *G. pallidipes* on p. 105 above. Amongst the animals present are bush-pigs (*P. koïropotamus* prob. *daemonis*), bushbuck (*T. scriptus* prob. *olivaceus*), red forest duiker (*Cephalophus natalensis harveyi*), common or savanna duiker (*Sylvicapra grimmia*), and a small antelope not yet shot but almost certainly the Suni *Neotragus moschatus deserticola.* Buffalo (*Syncerus

cafer radcliffei) and elephant use the thickets in some numbers for part of the year. Snakes are particularly numerous.

The adults of *G. austeni*, which I took, were as follows :—

In Kilosa (with D. W. Bishopp): in and beside closed, secondary, evergreen lowland forest, fairly open below, all but the largest trees of which were alleged to be 40 to 60 years old, on what was once cultivation on alluvium; heavily shaded but not very dense below; much broken at present and old and new cultivation adjoining, also *Acacia* savanna; the fauna consisted of bush-pigs (especially), monkeys (*Cercopithecus leucampyx* and *aethiops*), bushbuck, and baboons. At dense, small arbours formed in very open fallow on alluvium, with scattered trees and (seasonally) very high grass; in one case actual cultivation, by a luxuriant cucurbitaceous climber that had enshrouded dead trees; the fauna consisted of wandering bush-pigs and an occasional bushbuck. In a fairly open grove of *Acacia campylacantha*, with small patches of climbers and of other dense growth, on a limited patch of alluvium on a hill-side, surrounded by *Isoberlinia–Brachystegia* wooding.

In Mozambique, just outside a stream-fringing, closed forest, perhaps a hundred yards wide, which consisted of savanna under long-standing re-invasion by evergreen lowland rain-forest elements and which was, in effect, not very different from the above locality at Kilosa either in shadiness or in density near the ground. A native described these small tsetses as sometimes becoming abundant even at man in this part and as differing from *G. brevipalpis* in following out of the fringing forest into the open savanna at any time of the day. The fauna consisted of bush-pig, bushbuck, numerous blue duikers, monkeys (*C. leucampyx*), baboons, sometimes buffalo, and occasionally elephant. The particular fly taken here came to a native feeding flies on a goat, but the goat was neglected.

I have seen the Nyusi country, near Korogwe, in which Morstatt took his dozen examples of *G. austeni* in 1913. This locality is worth describing as a type of the haunt of this fly. It contains ample vegetational interspersion of types suited to feeding and breeding. Shady thickets, with some high trees overtopping them, mark brokenly the course of the streams; and even in the open short grass-land of limited width through which in places these streams flow, and which could be used as feeding-grounds, there are clumps of savanna wooding in which, as in the more extensive savanna wooding which encloses the whole, there are numerous " arbours " formed by cucurbitaceous and other climbers, of the type so popular in Kilosa. Rubber plantations, totalling approximately 300 acres, are present and are to-day infested with tsetses.

(b) The rest-haunt and its furniture.

It may be concluded from the evidence summarised above that the rest-haunt or " home " of *G. austeni* is supplied by closed thicket or forest, fairly dense, of varying secondary types, and by plantations giving equivalent conditions; and that true and extensive rain forest, where intact and unvaried or very densely regenerated, is not included.

We may assume that the females will use for resting the undersides of the rocks and logs under which the pupae have been found, but no direct observation exists for either sex of this species.

(c) The breeding-grounds and their furniture.

I took pupae in far greater numbers than adults in each of the sites above mentioned. Wallace, as stated above, found pupae in only two of his types, but adding these to Bishopp's, and Moggridge's findings and my own, it is suggested that most of the types of cover which are suitable for the rest-haunt are suitable for breeding as well. The breeding and resting haunts are rather more like those of *G. pallidipes* than of *G. brevipalpis*, though to some extent they are intermediate.

My pupae were mainly found under logs, including a great uprooted tree lying head-down in a fairly open donga leading to a river with dense wooding; beside it I noted evidence of the rootling of pigs. Beside another were the old tramplings and lying places of elephants. Others were in the closed forest of locality (iv) above. The general country between and near the sites in Portuguese territory was open, with *Terminalia sericea* savanna, some thicket of *Markhamia* and *Bauhinia*, and short grass with stretches of longer grass. From under one large log near Kilosa in evergreen lowland forest * nearly 300 empty pupa-shells were taken. Of Wallace's 261 puparia, 170 were collected from two square feet of ground under one large overhanging rock. Altogether he found puparia in seventeen spots, in sixteen of which the shelter was provided by rock. In the seventeenth, 20 pupae were found under a fallen trunk. The ground was always sandy, dry, and incapable of being inundated. Humus to a depth of two inches was in many cases present. Moggridge's pupae in Kilifi were found in "elephant thicket." He had found many pupae in Kiwanda (in the damp valley between Bulwa and Mlinga, below Wallace's mountain-side sites) in the following localities :—

(*a*) In a lightly wooded area east of the mission :—	
in the base of the thicket growth	1
in the base of a rotten standing stump . . .	8
in the base of a large, upright growing tree . .	14
(*b*) On the higher slopes of riverine forest in the same locality :—	
in thicket bases	32
in the bases of standing trees	13
(*c*) On the lower slopes of riverine forest, near river :	
in rock sites	20
in the base of trees	19
under a large, long, exposed surface root . .	97

Both in this locality, and in Kilifi, though he took numerous adults of *G. brevipalpis* and *G. pallidipes* and hardly saw *G. austeni* at all, almost the only pupae which he could find, and these in great numbers, were those of the last-named species.

(d) The feeding-grounds.

If the analysis suggested above is approximately correct, very open wooding and open margins are capable of forming feeding-grounds for this species, in which the loitering male population will mingle with the hungrier males and females and exceed them in numbers. Still more open plantings and open cultivation are normally visited by the hungry flies only, though in Wallace's case only by females.

It is, on the other hand, fairly certain that where a habitual concentration of food animals takes places in one spot in dense wooding—even within

* Referred to at the top of p. 118.

the margins of rain forest—that spot can become a feeding-ground, and its surroundings a resting, mating, and breeding-ground; this appeared to have happened near Zigi in 1926 at a spot in regenerating forest, where, under a mass of great rocks, bush-pigs regularly rootled and slept. This may happen also in the case of *G. palpalis* and *G. brevipalpis*.

This was apparently also the case in a situation investigated by Burtt in 1935, during the writing of this report. The following summarises his account of it:—

The Ngerengere river near Kingolwira, 14 miles from Morogoro, swings north for about 10 miles past the isolated inselbergs of Mkumbu and Mbokwa. It passes here through dry deciduous *Acacia-pallens–Combretum* savanna of density 5–6 (*see* p. 31 above) throughout the 8 miles investigated. This savanna is broken by occasional thicketed tributary gullies, largely characterised by *Acacia pennata* and *Cissus rotundifolia*. Scattered baobabs and candelabra euphorbias stand out of the thicket here and there, and the undergrowth contains an impenetrable barrier of spiny sansevieras. The savanna is infested with *G. morsitans*.

The river itself is hidden by a thick evergreen fringing forest of large trees forming a wall 80–100 feet high, the width of the forest being from 200 to 300 yards. Its character is that of the forest in Mozambique referred to on p. 118 above. Though it is dense, it consists of a mixture of large savanna trees with a few rain-forest species. Overtopping it are occasional giant *Khaya senegalensis* or *nyasica* and *Sterculia appendiculata.* The forest is shut in by a wall of such climbers as *Landolphia Kirkii* and the shrubs *Acalypha ornata* and *Piper* form undergrowth. In the deep shade no grass is found, but there is an ivy-like carpet of dark green leaves of *Culcasia scandens*, while under the densest thickets the ground is littered with leaf-mould and rotting twigs. To penetrate this with cattle, a path had to be cut.

During five days, 25 hours were spent searching for tsetse with two bait-cattle, and much time was spent also in reconnoitring the outside of the forest, including the now nearly leafless thicketed ravines. In all, 28 *G. austeni* were taken, of which 19 were females and 9 males, in every case in the deepest shade under umbrella thickets, and usually after the bait-cattle had been standing for some time.

"From the scanty evidence available it appeared that during the severe day conditions prevalent along the Ngerengere river at this time of the year *G. austeni* lives in the cool of the deepest forest shade—whether it comes out to feed along the edge of the forest in the cool of night is not known" (Burtt).

Vegetational interspersion was present but was not seen to be used. Bush-pigs were abundant in the forest and were doubtless being utilised, as at Zigi. It is important to note that the flies in the forest were the reverse of hungry, coming even to the cattle with reluctance. They were obviously in their rest-haunt.

The flies were captured as follows:—"22 on the oxen and 7 on herbage near the oxen. Of the 22 flies all, with the exception of one on the belly and one off the rump, were taken just above the hoof and on the shank of the animals" (Burtt).

5.—THE PHYSICAL FACTORS.

(a) The geological and elevational habitats as indicators of physical factors and of the general climate of *G. austeni.*

The finds of *G. austeni* and its pupae hitherto have been between coast-level and 3,000 feet. The climates of Mombasa at one end of the latitudinal

scale and of Zululand at the other indicate the extremes of standard climate encountered by this species. The temperatures of Zululand have been mentioned under *G. pallidipes*. As regards humidity and lack of it in the general climate, the range runs from coastal Kilifi and the rain-forested Usambaras to the fairly dry thorn-bush climate of Kidete.

(b) One of the standard climates under which *G. austeni* flourishes.

The following are the average temperature and rainfall records obtained over the five years 1906–1910 (4 years only for June) by German observers at Zigi, where Wallace investigated this fly. I am indebted to Mr. R. E. Moreau, the Secretary of the Amani Research Institute, for the loan of the volumes (**22–25**) of the " Mitteilungen aus den deutschen Schutzgebiet " from which the figures are condensed.

TABLE 12.

Average monthly temperatures and rainfall at Zigi, Tanganyika Territory, in the period 1906–1910.

Month	Maximum temperature in degrees Centigrade	Minimum temperature in degrees Centigrade	Daily variation	Monthly variation	Rainfall in inches
January . .	29·9	20·3	9·7	12·7	4·2
February .	31·1	20·2	10·9	15·1	2·3
March . .	31·0	20·7	10·2	15·4	6·2
April . .	27·9	20·5	7·3	12·6	11·4
May . .	25·8	19·3	6·5	10·5	12·6
June . .	25·0	17·8	7·2	11·1	3·4
July . .	24·6	17·3	7·3	11·9	3·42
August . .	24·4	16·5	7·9	12·7	2·2
September .	25·5	16·8	8·7	13·4	2·1
October . .	26·9	17·3	9·4	15·0	5·4
November .	28·5	18·7	9·8	15·5	6·2
December .	29·5	19·9	9·5	12·7	5·4

The equability of the climate is remarkable, but this is by no means characteristic of all *austeni* climates.

(c) The eco-climates affected by *G. austeni*.

The very small differences found by Moreau to exist between the conditions in a coffee plantation and those recorded at the main (open) station at Amani, 120 feet lower, suggest that for practical purposes the standard readings at Zigi, summarised in the table just given, represent very fairly the " screen " conditions to be found in the more open feeding-grounds of *G. austeni* at the foot of the eastern Usambaras.

Moreau's own observations concern rain-forest types that appear to be avoided by *G. austeni* where unbroken, but are utilisable when in fragments. It has been mentioned that continuous rain forest of the type which Moreau calls " intermediate," though thoroughly searched with bait-cattle on traverses totalling 20 miles, produced only two flies. His " lowland forest " type, with its more open and uneven canopy, is judged to be not very different as regards the conditions which it provides from the regenerating rain forest near Zigi in which Wallace took 12 *G. austeni* females. The figures given in tables 13 and 14 below have been worked out approximately from thermohygrograph charts,

kindly lent by Moreau. These are taken from this "lowland forest" at a point close to Zigi itself. It will be noted that the daily periods, selected to show different combinations of temperature and humidity, are divided in unusual fashion, a period from 8 a.m. to 7 p.m. (just dark at Wallace's season), representing broadly what is believed to be the active period for *G. austeni* and (more broadly) the quiescent hours for *G. brevipalpis*, and another period from 6 p.m. to 8 a.m., representing the apparent time of activity of the latter, at any rate on moonlight nights.

It is intended mainly to emphasise the view that the 24-hourly means which are usually taken do not give a true picture of the conditions that affect a fly species. It is in the hours of activity that most fat is consumed, and these hours are the important ones to consider.

TABLE 13.

Average monthly temperature and humidity in "lowland forest" near Zigi, Tanganyika Territory, for the daily period during which *G. austeni* and *G. brevipalpis* respectively are believed to be active.

G. austeni active, *G. brevipalpis* resting in forest. 8 a.m. to 7 p.m. (mainly day).			*G. austeni* resting in cover, *G. brevipalpis* active outside. 6 p.m. to 8 a.m. (mainly night).		
Month	Temperature	Relative humidity	Month	Temperature	Relative humidity
1932			1932		
March	75° F.	77%	March	74° F.	85%
April	73° F.	85%	April	72° F.	87%
May	71° F.	89%	May	70° F.	91%

TABLE 14.

Temperature and humidity in "lowland forest" on certain dates near Zigi, Tanganyika Territory, for the daily period during which *G. austeni* and *G. brevipalpis* respectively are believed to be active.

	G. austeni active, *G. brevipalpis* resting in forest. 8 a.m. to 7 p.m. (mainly day).			*G. austeni* resting in cover, *G. brevipalpis* active outside. 6 p.m. to 8 a.m. (mainly night).		
Date	Temperature	Relative humidity	Saturation deficit	Temperature	Relative humidity	Saturation deficit
			Low temperature and high humidity.			
15.viii.31	66° F.	92%	1·41 mm.	64° F.	92%	1·35 mm.
			Low temperature and low humidity.			
12.ix.31	70° F.	76%	4·43 mm.	68° F.	81%	3·32 mm.
			High temperature and low humidity.			
28.i.32	78° F.	67%	8·73 mm.	78·5° F.	75%	6·42 mm.
			High temperature and high humidity.			
6.ii.32	75·5° F.	79%	5·15 mm.	76° F.	82%	4·41 mm.

Note. The saturation deficit is worked out for the two-hourly periods as shown on the thermohygrograph.

TABLE 15.

Average monthly temperature, humidity, and rainfall observed in the "lowland forest" near Zigi, Tanganyika Territory, in 1931–32 over the whole 24 hours daily.

Month	Mean monthly temperature	Relative humidity	Rainfall in inches at Nderema *	Rainfall in inches at Amani
1931				
June . . .	71	83	2·7	2·7
July . . .	68·5	86	4·0	2·99
August . . .	68	86	3·9	4·0
September . .	69	82	2·5	3·2
October . .	72	80	4·0	3·7
November . .	72	77	6·0	6·0
December . .	75	82·5	7·8	8·5
1932				
January . .	75	77·5	1·5	1·1
February . .	75	78·5	4·0	2·5
March . . .	74·5	81	13·6	16·3
April . . .	72·5	86	13·4	15·5
May . . .	70	90·5	15·0	16·7
June . . .	69	86	1·5	2·7

* Nderema is at the top of a high ridge overlooking at a fairly sharp angle the lowland forest, the latter being perhaps 1,500 feet below. Amani lies somewhat further back. Moreau's " lowland forest " should be regarded as a relative term, as actually it lies somewhat high, and I know of lowland types of close-canopied evergreen forest very different from it, and at considerably lower elevations. I am indebted to Mr. and Mrs. Korte for the Ndarema rainfall figures.

(d) The round of the seasons: its effect, the hours of activity of the fly, and the evidence of seasonal contraction.

Little is yet known on the first and third subjects. Wallace noted that " the limits of both *G. brevipalpis* and *G. austeni* contracted when the heavy rains had given place to periodic showers," but late dry-season observation would be necessary fully to establish contraction and also to ascertain whether rain forest, regenerated secondary rain forest, and heavy gallery forest on streams might not then become the main refuges.

The hours during which this fly attacks in the open and its predilection for thicket, together with the German records referred to above and Moreau's, constitute at present our only indications of the temperature and moisture requirements of *G. austeni*. Attack may take place at any hour of the day, to judge from the observations both of Wallace and myself. " *G. austeni* varies little from hour to hour " (Wallace). This indicates a " drought tolerance " approaching or surpassing that of *G. pallidipes* rather than one equivalent to that of *G. brevipalpis*.

6.—GRASS FIRES AND THEIR PREVENTION AS A MEANS OF FLY-COVER CONTROL.

Where *G. austeni* is based on evergreen or extensive thicket, grass fires, normal or organised, are quite unlikely to affect it. Whether, and in how long a period, failure to burn will produce a sufficiently universal advance of the succession to extinguish *G. austeni* by densifying the bulk of its feeding-grounds

can only be ascertained by experiment. It is thought probable that in much country it will, but the problem is the same as that of *G. pallidipes.*

7.—THE MATING ORGANISATION AND DISPERSAL OF *G. AUSTENI.*

Little is known regarding the mating organisation and dispersal of *G. austeni*. That the fly will travel on animals was shown in Wallace's work. *G. austeni* is certainly less enterprising than *G. pallidipes* and probably goes less far from its thickets, for, with *G. pallidipes* at Zigi in the same numbers as *G. austeni* or *G. brevipalpis*, cattle could not have been kept either at Amani or Nderema.

8.—SUMMARY AS REGARDS *G. AUSTENI.*

Our combined observations regarding *G. austeni* present the picture of a fly probably less far-ranging and venturesome than *G. pallidipes*, but much more so than is *G. brevipalpis* by daylight; of a fly which, like *G. pallidipes*, is based on fairly dense thicket, whether extensive (but broken) or scattered, and breeds therein, but sallies to seek for its food in country devoid of undergrowth, or with open spaces interspersed, outside the thicket; of a fly, that is, which possibly could be successfully attacked by the removal, isolation or sufficient modification of one type of vegetation only out of the two broad types probably required. Closer observation and experiment may possibly show (*a*) that in districts with a severe dry season, thinning of the heavier coverts only—or their segregation—will suffice, though even this will be expensive; and (*b*) that densification of the feeding-grounds by not burning the grass may be useful.

9.—THE ECONOMIC IMPORTANCE OF *G. AUSTENI* AS DEDUCED FROM OBSERVATIONS IN TANGANYIKA AND FROM ITS DISTRIBUTION.

Of the capacity of *G. austeni* to infect animals little is actually known, but Filleul reported from Jubaland that it is there regarded as specially deadly to cattle. Its capacity in practice to carry man's infections must be *nil*, since it practically never attacks him. It is most noteworthy (and typical) that throughout Wallace's month at Amani only one *G. austeni* came to man; the remaining 420 were all taken off the bait-cattle.

However, it is well to note also that *G. austeni*, almost never seen by man and therefore escaping notice and regarded generally as of negligible importance, has nevertheless been shown to be numerous in all suitable parts of the broad coastal belt (and at Morogoro, Kilosa, and Kidete—up to 150 miles inland) that have been well searched for its pupae, from Italian Somaliland to Zululand. Neave found it at Voi and near Witu and regarded it as well distributed in the Kenya coast belt. Morstatt, the German Entomologist at Amani, collected it at Nyusi, near Korogwe, and it probably occurs all round the two Usambara Ranges. Moggridge has taken this species at Kiwanja, between Bagamoyo and Pangani, as well as in some of the localities mentioned earlier. I obtained it also at the foot of the Nguu Mountains in Handeni.

Further, this fly comes with readiness to bait-cattle, and wanders outside its thickets at any hour of the day; so that it may prove to be a much more important excluder of stock than has been realised, masked as its effects must be also by the fact that it occurs everywhere in company with less retiring species.

It is proposed that Moggridge should study *G. austeni* at Kilifi, incidentally to his study of *G. pallidipes.*

I.—THE RELATION OF *GLOSSINA PALPALIS FUSCIPES* * NEWSTEAD TO ITS INANIMATE ENVIRONMENT.

In our work on *G. palpalis* in Tanganyika we have concentrated on two small islands, Riamugasire and Maboko, both in the east of Lake Victoria, the conditions on which are drier, to judge from the vegetation, than on the islands on the Uganda side. Our own observations will here be combined with extracts from some of Fiske's and Carpenter's publications to provide a more complete summary of the known habits of this fly. It should be noted that the conditions even on our islands are very different from those obtaining, for example, on the streams of the Sudan–Uganda border, with its marked wet and dry seasons.

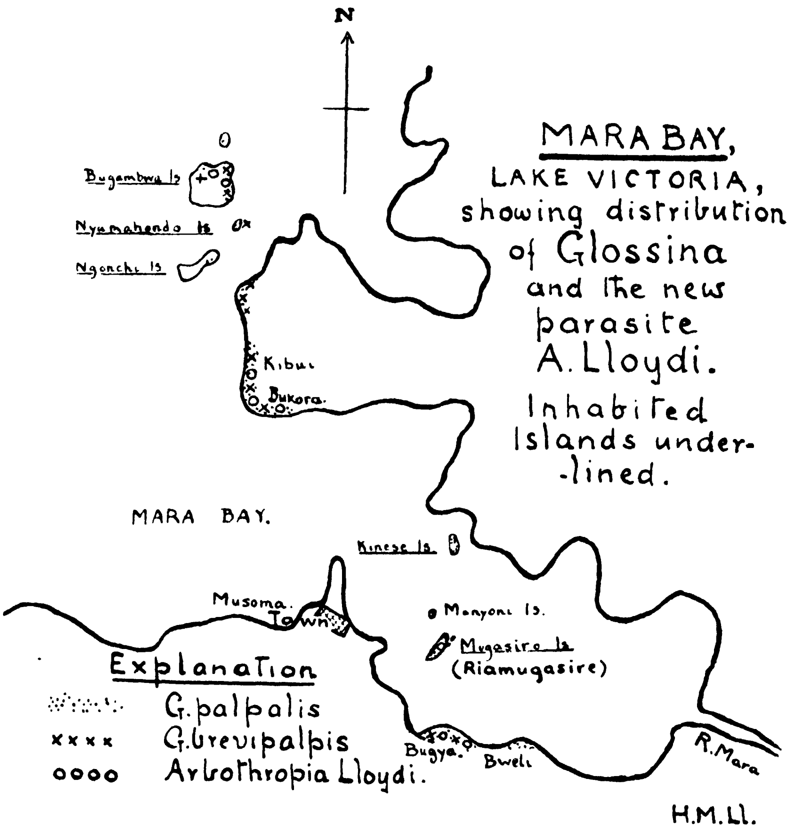


FIG. 11.—Sketch map of Mara Bay, Lake Victoria, showing the distribution of *Glossina palpalis* and *G. brevipalpis* and of the parasite *Arbothropia Lloydi.*

1.—THE VEGETATIONAL TYPES WHICH *G. PALPALIS* CANNOT INHABIT.

This species, it appears, cannot inhabit any vegetational type if separated from the shore by an adequate and complete clearing, unless (in rare cases) special facilities are present for an independent inland colony, like that

* The form of *G. palpalis* infesting Lake Tanganyika has recently been described as *G. martinii* by Zumpt. *See* appendix 10.

found by Fiske on Mbugwe Island (Fiske, 1920). Adequacy will vary with conditions.

Forest of the densest type—Burtt's density no. 1—(*see* p. 31 above) in sufficient width is unsuited to this fly. Chorley of Uganda regards this type as exclusive of *G. palpalis* in the islands in the north of Lake Victoria. Fiske (1920 : 385) regarded " the very dense forest which clothed the slopes of the hill " on Mbugwe Island " as a strong deterrent to dispersion of the fly. . . . They were walled in by it." Johnson & Ll. Lloyd (1923) considered that " it is of great importance that *palpalis* is very scarce in excessively dense rain forest. . . . A broad road cut through such a forest does not satisfy [its] requirements and, so far as we have seen, village clearings in the heart of it are uninfested by the fly except for rare stragglers. . . . Like *palpalis*, *tachinoides* is absent or very scarce in forest so dense and tangled as to be almost impenetrable." " Vegetation which grows too densely is not associated with the presence of great numbers of the fly." Papyrus (see below) is given as one example (Carpenter, 1919 : 3). In dense vegetation the flies use the hippopotamus tunnels if there are any. " A shore along which the forest comes as an impenetrable wall to the water's edge . . . does not offer the best conditions " (Carpenter, 1919).

In the fly rounds on Riamugasire Island merely an odd fly was taken in the sections which traversed the continuous, uniform, dense dry thicket. No breeding was found taking place there.

Fiske showed that, given certain conditions which are rare in east Africa, there is no reason why this species " should not be found at any distance from the water front " (1920 : 385). To say, therefore, that *G. palpalis* cannot inhabit wooding otherwise suitable for more than a given distance from the shore would be untrue; but under the condition of lack of suitable food animals, with localised and regular habits, it cannot do so.

Open savanna wooding back from the shore or from the shore thickets is not inhabited, though odd flies are carried into it on man, and probably on animals, for considerable distances.

This species cannot inhabit a papyrus swamp if barred off from the rest of the water-front. Again, a broad and wide sudd belt not traversed by hippopotami or crocodiles is free from fly on its landward side (Fiske, 1920). Carpenter (1924 : 197) gave instances of population taking refuge safely behind broad papyrus belts in Central Kavirondo during the great sleeping sickness epidemic in the first years of this century, while the villagers in the intervening unprotected shore reaches died out.

A bare rocky coast is unfavourable (Carpenter, 1919).

2.—THE VEGETATIONAL HABITAT OF *G. PALPALIS*.

G. palpalis is, in practice, rarely found far from water. It is, moreover, never found far from woody or at least rank herb vegetation.

Its vegetational habitats on three types of islands in Lake Victoria is described below. In addition, a very different habitat occurs even on the shores of Victoria from the Kenya–Uganda geographical boundary eastward—dense, dry scrub of thorn-bush bound together by creepers (Carpenter, 1924). Carpenter (1919) regards *Alchornea*, *Triumfetta* and *Amomum* as affording very favourable shelter, where not over-dense; these represent, however, but one or two of a great number of types that are used.

G. palpalis occurs in strips of closed forest or thicket following rivers and even small streams traversing otherwise open country. The strips may be

narrow or broad, broken or continuous, as may be seen on the Kuja. In Nigeria (Johnson & Ll. Lloyd, 1923, pl. 18, fig. 1) it was met with even on permanent torrent streams lined narrowly by dark-leafed evergreen trees and traversing open or sparsely wooded hill country. This may be compared with the *morsitans* position at Gigoma (*see* p. 339 below) and contrasted with Jackson's observations on *G. swynnertoni* in Musoma (also p. 339 below).

Exceptions occur, for *G. palpalis* has been taken by several observers (see Newstead, 1924) in places as much as a mile from water, and where this phenomenon occurs it is probably associated (*a*) with specially damp zones (Hubert, 1907; Kinghorn, 1911), (*b*) with great numbers of food animals (Fiske, 1920), or (*c*) with temporary carriage (Fiske, 1920, and our own observations). Fiske observed: "Wherever leopard is absent and situtunga present [in consequence] in sufficient density, range of fly is extended inland. . . . There would be inland extension of infestation to approximately 5 times its present depth at many points . . . if it were not for the deprivative effect of the activities of leopards." This would be much deeper if there existed a suitable combination of vegetation and food. An opposite effect of the absence of leopards is discussed on p. 281 below.

Fiske also found a number of special concentrations of flies, with breeding-grounds complete, at varying distances inland. One on Mbugwe Island which was characterised by dense forest round an open space on the crest of a steep hill, fully 800–1200 yards from water and which was the haunt of numbers of *Varanus* (monitor lizards), was specially notable as being apparently completely cut off from the Lake.

3.—THREE TYPES OF ISLAND INHABITED BY *G. PALPALIS*.

(a) The islands of Uganda.

These islands present rings, broad or narrow, broken or whole, of dark green close forest, their outline diversified by indentations and capes, from the centre of which rise open grassy hills. Except in Bunyama and parts of Bugala which are underlain by ancient gneisses and schists, all the rocks outcropping in Sesse and Kome are quartzites and shales (Simmons, 1926 : 19, 20), though cliffs and gravel terraces of concretionary ironstone also occur. The soils are for the most part loams, well mixed with humus, where they are under shade.

The forest, in which large-leafed *Anthocleista*, *Moesopsis Eminii*, several large species of *Ficus* and the smaller *Markhamia platycalyx* and *Teclea nobilis*, are amongst the more prominent species, is of fair height and of damp and tropical appearance. It varies in density even within small areas. It may reach to the water's edge or be separated from the latter by a sandy beach, which in turn may be open or may support a growth of shrubs (most commonly *Alchornea cordifolia*) and may occur also along stretches of forestless shore. Rock shores are not uncommon. In places, the shore may be separated from the water by a bed of sudd, which is often traversed by the water-paths of hippopotami and crocodiles. Some islands are nearly covered by the forest. In the more usual type, the grass hills rising above it may be either open, or parkland, or may support in addition patches or stretches of dense thicket, and hippopotamus tunnels may traverse the dense vegetation for considerable distances from the shore. With the lake-level low, an old beach-line of sand or gravel may be found, more or less overgrown, up to 100 or even 200 yards back from the water.

The animals—food and "indicator"—crocodiles and monitor lizards

(*Varanus niloticus*) are varyingly abundant; the lizards eat the eggs of the crocodiles and, very often, where lizards are abundant, crocodiles are scarce; Situtunga antelopes (*Tragelaphus spekei spekei*) frequent the interior of the islands on which they are found as well as their shores, unless man be present in force; in this case, reduced in numbers, they are confined to the marginal swamps. Hippopotami are varyingly present, as are monkeys (*Cercopithecus aethiops centralis*), bats, including large colonies of fruit bats (*Epomophora*), and on some islands shrews, some rodents, bushbuck (*Tragelaphus scriptus dama*) and waterbuck (*Defassa*). There are otters (*Lutra maculicollis*) and water mongooses (*Atilax paludinosus*). In some of the islands are domestic pigs, gone wild. There are many bird-colonies of egrets, comorants and darters. The butterflies are largely those of tropical rain forest.

The average temperature is higher than on the mainland, but climate and rainfall are more equable.

Detailed comparative studies of the Uganda islands, as regards tsetse, were made by Fiske and by Carpenter and may be found in the publications listed under their names in appendix 2.

(b) Maboko Island.

(map 1.)

This is a rather low island, one and a half miles long, situated in the Kavirondo Gulf, 15 miles west of Kisumu. It would be boat-shaped as seen from the air, if it were not for a large recurved promontory which projects from its northern side. The shore strip is narrow and the sides of the island rise from it sometimes steeply to a levelled-off top. There are two small hills, the smaller on the promontory, the larger on the island proper just east of the promontory. The larger hill was terraced by means of lava stones built into rough walls by the natives who inhabited it before the great sleeping-sickness outbreak of the first few years of the century. The island is now uninhabited except by our fly boys.

The rock is lava, and the soil is a clay, derived from it, which quickly forms heavy clods on one's boots, making Maboko a most unpleasant place in wet weather. Across the low neck of the promontory lies a deposit, relatively bare of vegetation, which is yielding many large mammalian fossils.

There is an almost complete lack of massive forest, though this was postulated by Fiske as a need of the fly. There are, however, two or three clumps of it, close to the shore, consisting of figs and *Albizzia* overshading fairly dense, damp thicket, and the latter, of quite rich type and probably equivalent to massive wooding, lies just behind the shore at other points in the island. Its chief constituents here are a *Grewia*, and a *Teclea*, with *Anisophylla*, *Sanseviera*, and *Aloë* also abundant. Rocky points occur, east and west, and elsewhere papyrus and ambatch (*Aeschynomene*), a narrow and much broken band only, fringe most of the shore. Lining the bay which nestles between the west side of the promontory and the island proper there is a wider accumulation of sudd. Rocky foreshore also occurs.

The lower part of the sides of the island is clothed with dry thicket composed mainly of the species which form the damp thicket below; *Anisophylla*, however, falls out and aloes become more prominent. Higher up the sides and top carry also this thicket, which is still "dry," but is broken up into clumps with broad passages and broader openings between of the semi-grassless lava clay. Large euphorbias of the *trilocularis* type * are dotted singly and in

* See pl. 15, fig. 1.

clumps through these thickets. The dry thicket becomes more continuous on the main hill and more interspersed with the thorny rambler *Acacia pennata.* This dry thicket was found to have a very much lower humidity than the damp thicket. *Acacia seyal* and *Balanites* sp. occur as trees in the open spaces of the upper parts of the island.

There are many crocodiles and monitor lizards on Maboko. A few hippopotami live off the shore, land on it at night, and sometimes wander over the island. The spoor of one situtunga only has been seen. A guinea-fowl was seen and a water mongoose. Three water-bird colonies exist. There are few butterflies on the island, though savanna-type Pierines are present.

The impression given by the island is one of dryness, except immediately on the lake shore. Sandy beaches are absent—at least under present lake conditions.

Fly boys, two of ours and one employed by the Medical Entomologist, Nairobi, under Milambo Kazila, one of the former, have been stationed on this island since November 1933. They attend to the traps, carry out fly rounds twice a week, marking the flies, not killing them. In addition, twice a week they search for pupae, which, after being recorded, are returned to the soil.

(c) **Riamugasire Island.**

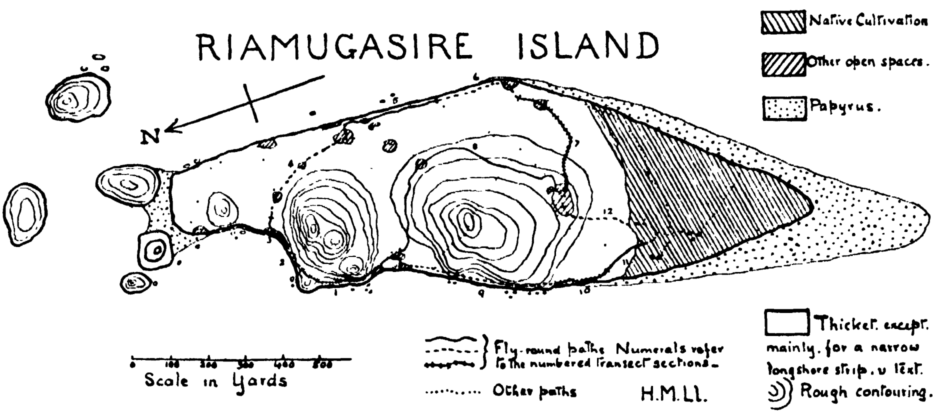


FIG. 12.—Sketch map of Riamugasire Island.

Riamugasire is a narrow island, about $1\frac{3}{4}$ miles in circumference, lying approximately two miles east of Musoma, with its long axis running with the meridian, and about half a mile from the nearest point on the south shore of Mara Bay. The whole was formerly settled, as may be seen from the stone-terraced hills, like that of Maboko, and the scattered grinding-stones. Since its desertion, it has gone to dense, dry, rather low thicket, which covers most of it continuously to-day except at its southern end. Proceeding north from this end one passes (i) a considerable bed of pure papyrus; (ii) on reaching land, a strip of cultivation by a dozen natives, the first of whom arrived nine years ago; (iii) the denser thicket just mentioned, which is described more fully below; and (iv) two small hills, occupying the northern third, also with dense vegetation, but, like that of parts of the shore, of a richer yet more traversable type.

Five little islets lie just off the north-west of Riamugasire from which they are separated by papyrus or channels. One of these consists of plain rock on which a number of crocodiles commonly bask simultaneously. The shores

of the mainland are very visible from Riamugasire, both to the north, where Kirure Isle forms a stepping-stone, and to the south (much nearer). Rocks jut out of the water off-shore and form further basking places for crocodiles. The rock is granite and the soil, derived from it, very sandy.

The usual ambatch (*Aeschynomene eraphroxylon*) characterises much of the shore, and the south of the island terminates in a large bed of papyrus. On the dry land the vegetation, as indicated above, consists mainly of dense xerophytic thicket with much " wild sisal " of the long bayonet type (*Sanseviera* sp.), *Aloë* and " Manyara " (*Euphorbia Tirucalli*); also *Lannea fulva, Commiphora pilosa, C. Eminii*, a *Flueggia*, some *Rhus glaucescens*, a *Euphorbia* of the *nyikae* group, and, of climbers, a fleshy *Cissus*, an *Asparagus*, and *Acacia pennata*. The *Cissus*, with a tall *Kalanchoë*, the *Sanseviera* masses and the *Aloë* indicate the dry soil conditions. At the southern end, near the cultivation, the mixture gives place to nearly pure Manyara thicket. It will be seen below that this vegetation is apparently exclusive of the flies. Some large fig trees are present, near the water's edge, in a few places. Small grass openings occur here and there, and where these are near the water they are favoured by crocodiles for basking. There is little or none of the " massive wooding " postulated by Fiske as necessary for the resting-haunts of *G. palpalis*, but the water-side sections which are overhung by large fig trees appear to take its place. *Acacia pennata* and an *Allophyllus* figure here in the associated thickets. Further details are given below of the trees that compose the rest-haunt (*see* p. 131).

The island has many crocodiles during a large part of the year. There are also a large number of *Varanus* lizards. A tortoise was also seen. Of the mammals, a hippopotamus frequents the island and a few " tumbili " monkeys (*Cercopithecus aethiops*) are present, while other hippopotami were seen on two occasions. The usual water-bird colonies are present.

The general aspect is dry, compared with that of the Uganda islands.

An attempt to catch out the flies on Riamugasire Island by hand was made by H. Koch from the 29th January, 1913, to the 31st January, 1914. Four expert fly catchers with nets were employed. In all, 74,382 flies were caught in 340 days, 49,883 being males and 24,449 females, a similar preponderance of males being maintained throughout the period. The largest average daily catch (541) was made in April and the smallest (78) in December. The average daily catch in January 1913 was 205 and in January 1914, 102; in January 1913 only three days were available. The flies were by no means exterminated (H. Koch, 1914).

Our own observations on Riamugasire started in March 1933, with the stationing of Lloyd in Musoma. The primary object of this was to test the usefulness of the parasite *Syntomosphyrum glossinae* on ground in which the pupae of *G. palpalis* were found almost entirely in humus. In addition a small meteorological station was installed on the island and readings and fly rounds, as well as special observations, were carried out regularly till December 1934.

4.—THE USE MADE BY *G. PALPALIS* OF THE PLANT COMMUNITIES WHICH MAKE UP ITS VEGETATIONAL HABITAT.

(a) The vegetational concurrence requirement in Uganda, and on Maboko Island, and on Riamugasire Island.

(i) *Uganda.*

Fiske (1920) stated that " Two kinds of shelter are requisite, (α) light, such as serves as breeding-grounds and for the active flies; (β) massive or forest-like, which is required by the inactive flies."

Both kinds must be simultaneously available. " Provided there is good shade the fly may extend its range to parts where there is poor shade " (Carpenter, 1919 : 3).

In the case of *G. palpalis*, Fiske, for each species studied, found like ourselves that the contact of the two types of vegetation required by it were in each case the point of its greatest density.

Jackson, following his visit to Uganda, summarised the use by *G. palpalis* of the vegetational communities, as known to C. W. Chorley and Hancock and shown there to himself, as follows :—

(α) The habitat is divisible into resting-haunts, breeding-haunts, and feeding-haunts. The breeding-haunt, at least when permanent, is part of the feeding-haunt, and not part of the rest-haunt as it is with *G. morsitans*.

(β) The rest-haunt has rather heavy shade; flies like to sit about on spots where the sunlight strikes through to the ground. One is not bitten in the rest-haunt, except by flies that may have followed in. Traps placed in the rest-haunt are ineffective, except on a fly roûte leading out of it.

(γ) Flies leave the rest-haunt with the onset of hunger every 2 to 4 days and seek the feeding-haunt. After engorgement they return with very little delay, unless *Bembex* wasps are patrolling the return route.

(δ) Permanent breeding-haunts occur on fly beaches, and form part of the feeding-haunt. At times of high lake-level most of these are submerged, and the fly resorts to temporary, scattered breeding-haunts; meanwhile the density falls.

(ε) One may pass from rest-haunt to feeding-haunt in perhaps five yards. There is practically no entomological interzone.

I made a sketch of Nsadzi as a record of common Sesse conditions. In this, just back from the lake, there runs a long white sandy beach, completely open, which forms the main feeding-ground. Along the back of it runs a continuous bank of Olu-zibaziba (*Alchornea cordifolia*) bushes. These are the breeding-ground and in part feeding-ground also. Behind the left of the *Alchornea* stands a low cliff—the " vine-clad cliffs " of Fiske. Behind its right there is a slope, which forms the bottom of a hill that runs from the cliff as well. The whole lower slope is covered in dark green, close wooding in which *Albizzia* sp. and *Anthocleista* sp. are conspicuous. This and the cliff supply the " massive " element to which the flies resort for shelter and rest. The top of the hill is open grassland.

In this case we have the zonal arrangement which characterises also Maboko, but the rest-haunt and breeding-ground are transposed.

Partiality to vegetational contacts (Leopold's edge effect; for the definition of this term, see appendix 1) is as marked in *G. palpalis* as in the other tsetse flies. " A forest of tall trees, without much undergrowth, is only productive of *Glossina* [*palpalis*] in any quantity at its edge, either along the water's margin, or, if a narrow strip bordering water, on its landward side. . . . Indeed it may be said to be characteristic of *G. palpalis* to be found in greatest numbers at the edge of open spaces backed by, or surrounded by, forest." Diminution of the flies as one enters the forest " is not merely due to the fact that one thus goes further away from the water, because in Bugalla in 1912 the same thing was noted in the strip of forest along the coast if one entered it from the landward side, the flies being more abundant at the edge than when one had penetrated a little way " (Carpenter, 1919 : 41).

(ii) *Maboko Island.*

The feeding, resting, and breeding-grounds occur here also in three concentric zones. In the former is included the lake edge and some open grassy " hippo " feeding-grounds just behind the papyrus or ambatch. Behind this is a discontinuous zone of well-grown and highly shady thicket which the flies use as their rest-haunt, but in which they also breed. Behind this again, on drained ground, rising sometimes steeply, sometimes gradually, are thickets of similar composition but drier and more stunted appearance. These constitute the largest breeding-zone.

(iii) *Riamugasire Island.*

The greater part of the homogeneous thicket, which characterises Riamugasire, is apparently unsuited to *G. palpalis*, only odd adults or pupae having ever been found there. Along the shore and on the two rises, interspersion with more open types was present and, therefore, flies were present also. The mixture was mostly too minute to be represented by separate sections of the fly round, and for this reason the actual sections showed mostly mixed results, and necessarily give very mixed figures, but there were sections of which it could be said that they were in the main feeding-grounds or rest-haunts respectively.

(b) The rest-haunt or base of the flies.

In such spots the flies shelter when inactive and emerge only when ready to find food or females, or to deposit their larvae. Light shelter suffices for the active flies, which only use it temporarily, searching for food (both sexes) or seeking females (males) and for breeding. Islands lacking heavier shelter lack flies also.

(i) *Uganda.*

Of the rest-haunt in Uganda, Fiske (1920 : 433) wrote :—" Massive or forest-like shelter must be had. It may not exist within several thousand yards of a point where fly occurs, seemingly well satisfied with its environment, but in such cases it will certainly be possible to trace the source of infestation to centres located close to the forest growth." Fiske defines massive shelter as " large trees in masses or very heavy masses of shrubbery. . . . A cliff overgrown with vines and shrubbery has been observed to serve as massive shelter." *Uapaca guineensis*, with high adventitious roots, is dominant in many such forest stretches near the lake, and *Maesopsis Eminii*, *Ficus sycamorus*, *Piptadenia Buchanani* and *Canarium Schweinfurthii* are common trees. Among the shrubs, *Lasianthus* is often dominant in the undergrowth of the forest, as is the climbing *Mussaenda arcuata* at its edges (A. H. Thomas).

(ii) *Maboko Island.*

On Maboko Island, the rest-haunt, which is the intermediate of the three zones referred to above, consists of damp thicket dominated, as stated already, by tall-grown shrubs of *Grewia*, *Anisophylla* and *Teclea*. *Rhus*, *Acalypha*, and *Allophyllus* densify it in parts and in a few places Albizzias of the *sassa* group and large figs overshade it. " It provides good canopy and a more or less open space below, in which *Sanseviera* is common. Flies are numerous in it and, in this type, are active from about 8 to 11 a.m. at temperatures from about 73° F. (wet bulb 66° to 68°). From 4 p.m. there is a resumption of activity, and flies seem slightly hungrier and more inclined to attack. Flies in the rest-haunt are very elusive, settling on trees (head down),

on twigs, leaves, and rocks, usually in small sunny patches. Hunger is slightly higher where the path passes through the rest-haunt. Few flies attack man. Some breeding was found to occur in the rest-haunt" (Jackson). Actually in typical rest-haunt sections just back from the shore on Maboko I found plenty of pupae. While I am satisfied as to the existence on Maboko of a restricted rest-haunt, I consider that on this island it is, at least in some months, completely overlapped by the breeding-ground. The table given on p. 135 below on the breeding-grounds on Maboko Island should be noted in this connection.

(iii) *Riamugasire Island.*

The water-side sections overhung by fig trees referred to already were mostly small and much separated and they therefore certainly did not monopolise the resting flies. They were, however, the nearest approach to the rest-haunt types of Uganda. They contained, in addition to the figs, lower and close growth of *Combretum molle* with occasional *Trichilia*, *Synadenium Grantii*, *Rhus glaucescens*, *Silicomorpha parviflora* and *Anisophylla*.

However, as H. Lloyd has written, "any portion of the path round Riamugasire Island is capable of acting as a feeding-ground as, in places inaccessible to crocodiles, *Varanus* and birds would be able to provide food. The thickets and trees bordering this path would be able to act as a rest-haunt. It is hard to conceive that flies feed in transect 6 (feeding-ground) and then travel half a mile or more to transect 2 (rest-haunt) in order to digest their food. It is more conceivable that they should fly to the thicket bordering the path to carry out this function. It was also much used by them for breeding."

(c) **The breeding-grounds.**

(i) *Uganda (Islands on Lake Victoria).*

Carpenter (1920 : 55–56) classifies the breeding-grounds of the Uganda Islands into two categories: (α) beaches near the water, well shaded and composed of sand and gravel, in association with which *G. palpalis* occurs in maximum numbers, and which he terms breeding-grounds, and (β), in their absence, scattered nooks—such as little pockets of humus and dried-up debris under angles of rocks or at the bases of trees—which he terms *loci*. The physical requirements he summarises as "loose dry soil, well shaded, but with the surface thoroughly ventilated, within a few yards from the water but beyond its reach. . . . The soil itself may be of diverse kinds: fine pebbles, pebbles mixed with coarse brown sand, coarse white sand, fine white sand (which lies too closely to be the most favourable medium (1919 : 43)), light friable earth, vegetable humus and debris, and the very fine dry dust found in caves and probably mostly derived from disintegrated droppings of bats. Coarse sand with or without pebbles has been found to yield the greatest number of pupae," especially where it forms old beaches at a distance back from the water. The flies can exist in certain numbers (say to a density of 13 per boy per hour) where there are no real breeding-grounds, but only *loci*. A dense layer of damp leaves on the ground is bad (Carpenter, 1919 : 44), a light layer good. A thick-leafed aromatic labiate, only three feet high, often shades numbers of pupae (1919 : 46). On this point, compare the relation of *G. pallidipes* to *Justicia* (p. 105).

Fiske associates breeding-grounds :—

1. *with the longshore course followed by the streams of moving, food-hunting flies.* Thus "the most attractive breeding-grounds are the deposits of clean

dry beach sand or gravel that occur more or less frequently along the shore . . . in or near to the course followed—and they must be shaded." Such beaches are sometimes as much as from 600 to 1,000 yards long.

2. *with feeding-grounds elsewhere also.* (i) " Much the largest deposits of pupae have been found within a few yards of crocodile nests, in the same type of soil and under the same type of vegetation " as that under which the crocodiles day after day brood over them, . . .; and (ii) " an almost equally striking correlation [exists] between breeding-places of tsetse in vegetable debris and basking spots of *Varanus* "—the lizards return daily to the same places; and (iii) large finds have been made in association with situtunga. At certain spots on the old beach line the antelopes had made open sunning-places for themselves by preventing new growth from springing up in openings left by falling trees. It was noted that in the breeding-places, which were in spots shaded by dead vine-tangles, fallen logs and tufted vegetation which had been spared, " the deposits of puparia were larger than could be found at any point along the shores." Again, on p. 421, Fiske noted that " it soon became evident that although the fly was to be found in maximum density along the open fly beaches, the great mass or body of the fly bred in the deposits of sand and gravel marking the old beach line, usually hidden from sight and anywhere from 10 to 100 yards back from the existing shore line." Ancient shore lines as much as 300 yards in were used in the same way.

Shade may be provided by caves or undercut rocks, prostrate trees, the hollows at the base of living trees, the disc of earth turned up with the roots of an overturned tree, and bushes. " These, especially the Oluzibaziba (*Alchornea*), provide shade all the year round, and if the soil and other conditions are suitable, pupae may always be looked for from them with success " (Carpenter).

" Vegetation not more than two or three feet off the ground, both shrubby and herbaceous, rocks, logs, stumps, etc., provide attractive shelter " (Fiske, 1920 : 412). " Such light shelter as is provided by low massed shrubbery with open spaces between thickets or clumps of it, masses or clumps of rank-growing herbs, vine-covered bushes, etc. . . . is the kind of shelter which provides shade for the most attractive breeding-places " (Fiske, 1920 : 428).

(ii) *Maboko Island.*

The main breeding-grounds are certainly in the dry thicket which extends brokenly from the edge of the lake to the top of and all over the island. On the sides and top of the main hill many live pupae and great numbers of cases were unearthed. Thorough searches were carried out by myself over paced-out pieces of ground from the 17th to the 19th January, 1933, (*a*) on the side of the hill, near the camp, (*b*) on the very top of the hill, (*c*) in the rest-haunt near the landing-place characterised by *Anisophylla*, etc., and (*d*) in closed thicket under good *Ficus–Albizzia* canopy, just back from the shore, such as would also definitely be classed as rest-haunt. The results obtained are shown in table 16.

It is suggested by the above that while, in the long run, the dry thicket and damp thicket (rest-haunt) vary little in the extent of their utilisation for breeding, the latter in January 1933 was being used more than the other in the ratio of about 6 : 1. The pupae and shells were found everywhere in the bed of humus that in all the thickets overlies the lava clay, but not in the clay itself. Flies were much less numerous (to man), yet apparently slightly hungrier, in the breeding-ground than in the thicket of the rest-haunt.

TABLE 16.

Numbers of pupae of *G. palpalis* found on Maboko Island under varying conditions.

Locality	Square yards searched	Total *palpalis* puparia	Puparia per sq. yard	Full *palpalis* pupae	Parasitised *palpalis* puparia
Hill-side (*a*) (dry thicket) . .	100	159	1·6	2	0
Hill-top (*b*) (dry thicket) . .	150	1210	8·0	25	11
Rest-haunt (*c*) (damp thicket) . .	200	586	2·9	81	2
Rest-haunt (*d*) (damp thicket) . .	100	913	9·1	93	4

The fact that the thickets of the entire island are used for breeding is extremely interesting in view of the practical confinement of the fly and its breeding to the zone next the water both on Riamugasire and on many of the islands of Uganda. The main difference between the tops of Riamugasire and Maboko is that on the latter the thickets are compact but have open rides and spaces between them, splitting them up, while on Riamugasire they are a continuous, homogeneous mass of somewhat lighter consistency. The only movements of food animals over the surface of Maboko known to occur are those of four hippopotami *at night*. It is believed that these are fed on in these hours by *G. brevipalpis*, but hardly by *G. palpalis*. It is fair to state that the centre of the island is nowhere more than a few hundred yards from the water.

The position on Maboko may be compared with that described by Fiske (1920 : 381) for Bukasa Island, with " a dry, hilly interior, with only a light infestation along shore, and for all this a general infestation of the interior," except that the long-shore infestation of Maboko is not light, that the inland infestation is certainly secondary, and that this island is far smaller than Bukasa, which is fully fifteen miles long by two broad. Again, " a remarkably heavy infestation was found on the very summit of a high hill near the centre of the southernmost peninsula on Bugala Island . . . heavier on the summit than the slopes " (Fiske, *ibid.* : 418).

Lake-level has been high during the period under investigation. Whether beaches will be revealed on Maboko by a fall remains to be seen.

(iii) *Riamugasire Island.*

(α) *Sites favoured and not favoured.*

The breeding-sites seemed to be scattered fairly evenly round the edge of the island except where the coast was rocky. Here few pupae were taken. The greatest number of pupae was taken under umbrella thickets, forming fairly continuous bands. These varied from one to five yards in diameter and cast a medium shade. The pupae were found for the most part between five and twenty-five yards from the water but (contrary to Fiske's experience) never in large numbers in the resting-places of crocodiles. The soil was sandy. Other favourable places were on the edges of the paths in the hippopotamus tunnels that ran through continuous thicket for a limited distance from the shore and at the bases of fig trees. The humus layer is continuous

under the thickets. Undercut rocks produced a certain number of pupae but not nearly so many as the thickets. Despite regular search, one puparium only was taken as much as 200 yards from the shore, but Nash, who first investigated the island, took many cases under liana canopy on the sides, and top, of the little hill.

(β) *Soils favoured and not favoured.*

"The most favoured soil was a deep, light leafy humus with a certain amount of fine sand. Where fine rootlets occurred in the soil the deposition was even better, probably owing to their draining properties. A pure sandy soil with from half an inch to an inch of humus on top proved very favourable, the pupae being found *in the humus.* This again was possibly due to its excellent draining properties. Pure sand without any humus very rarely produced pupae" (Herbert Lloyd, unpublished report, 16.iv.33).

(γ) *The effect of seasonal changes in shade distribution.*

In June (Lloyd reported) the canopy of the breeding-sites is still nearly uniform throughout. In August after considerable leaf-fall has set in, some of the thickets in which breeding has hitherto been taking place are nearly defoliated and become unfavourable for breeding. The latter then becomes much concentrated, being confined to the spots in which leaf still persists. The flushing of the trees in October causes pupae once more to be deposited over a wider area.

During the time of leaf-fall the most productive sites were the slopes of two ant heaps covered with light thicket which had retained their leaf. In a search of one hour and fifty minutes these two situations combined produced 1,514 empty cases and 284 live pupae of *G. palpalis* and twenty empty cases of *G. brevipalpis*. This represented a rate of nineteen live *G. palpalis* per boy hour. Ant-hill breeding-sites are no doubt favourable throughout the year, for it would be impossible for them to become water-logged during the rains.

The above should be compared with the observations made by Carpenter (1919): "Shade produced by fresh green growth . . . is at once made use of by the fly, for larviposition. Hence pupae may be found at different times in different places according to the local conditions of the vegetation. At other points the shade is always uniform and such localities are always suitable for pupae. Pupae are readily killed by diminution of the density of shade."

(δ) *Density of deposition of pupae.*

Thickets well carpeted with leaf humus gave (when in leaf) 63 live pupae and 800 empty cases of *G. palpalis* in one hour and forty minutes, a rate of six pupae per boy per hour. This was slightly above the average rate. A rough estimate by Lloyd of the area on the island used for breeding during the season of leaf showed it to be about 9,000 square yards. From average results obtained he would expect to find about two pupae per square yard of breeding-ground throughout this area. Pupae on Riamugasire are not found in large concentrations as is the case in Uganda, but are fairly evenly scattered. Thus with only two pupae per square yard an enormous area of ground has to be searched before a large number of pupae can be obtained. This also means that a parasite such as *Syntomosphyrum* that was released here in large numbers (*see* p. 242 below) has to search far before it can find a pupa to parasitise.

(ε) *Seasonal rate of larviposition.*

The greatest numbers of live pupae are found near the end of the rains.

(d) The feeding-grounds.

(i) *Uganda.*

There is a continuous longshore movement of hungry flies, with a high female proportion, up to considerable distances from the nearest *point d'appui* in the form of massive shelter. The lightly bushed shores and beaches are feeding-grounds for the flies, and the movement extends even along the front of otherwise highly unattractive stretches of sudd, lower densities but far higher female proportions characterising the types of shore that repel all but the hungry flies of both sexes. Continual movement by the latter was proved by Jackson, as it has been for our open *morsitans* feeding-grounds, by "standing catches" made in one spot. In such catches the density of the male flies—not of the females—was easily reduced even by one hour's catching, but the stream of hungry flies, with its high female proportion, went on indefinitely (Fiske, 1920). It was shown that the "degree of activity is correlated with abundance or scarcity of food. . . . When food is so scanty on an island that the female percentage [generally] is very high, it is impossible to reduce the local density of either males or females by catching experiments at the points they are passing." This means that both sexes are then seeking food.

The water itself at its margins forms a feeding-ground for *G. palpalis.* Fiske's famous canoe experiment first indicated this. The prow of the canoe was thrust through a dense but narrow strip of high reeds fringing the shore, the latter being a patch of open grass cropped by hippopotami and combined with attractive shelter for the flies. Collections, made simultaneously in the stern on the open lake and the bows on the land side of the reeds, produced during two hours a typical "feeding-ground" female percentage of *passing flies* of 68·2 to lakeward and only 14·3 to landward.

The concentrations of *G. palpalis* beside open spaces in the bush much frequented by animals have been referred to already. These then become feeding-grounds and such feeding-grounds are indistinguishable in kind from those of *G. morsitans.*

Fiske's resultant hypothesis, "which has withstood all tests," may be summarised as follows :—

(*a*) The active (*i.e.* hungry) flies are continually in movement and passing points along shore.

(*b*) These streams of flies consist of (i) food-hunting flies of both sexes, which move rapidly; and (ii) non-hungry male flies, seeking not food but females, which frequent the route on which they will find the latter but move much more slowly if at all.

(*c*) These lingering males delay where the vegetation is attractive and pass quickly, or not at all, the points where it is unattractive. The hungry stream searches all types of margin.

It follows therefore that the density of males will be greatest where vegetation is attractive and the percentage of females, caught at man, will be highest where the shelter is least.

The movements are along shores of lake, banks of streams, contacts of woodland with more open country, gamepaths and footpaths; and, in general, they "follow quite closely the line separating sunlight from shadow.

The flies are averse to penetrating shadow, unless sunlight is perceptible beyond" (Fiske, 1920: 369 and 74).

(ii) *Maboko Island.*

To judge from the immense numbers of females caught by our traps, the short-cropped grassy spaces which the hippopotami kept open in places between the shore ambatch and papyrus and the drier thickets on the foot of the rise or on the lake shore itself, were feeding-grounds of the flies; but the fact that, like the Uganda beaches and the hard-pan strips of *G. swynnertoni*, they were overrun also by loitering males, masked the high female percentage of the hungry flies from the hand catchers. Breeding was taking place in the bush alongside, whether rest-haunt or drier true breeding-ground.

The open spaces of the high parts of the island were not seen to be used either as feeding or sex-assemblage grounds, though there were pupae in the thickets. The water-surface along the shore was probably used as a feeding-ground. Jackson obtained this result:—

TABLE 17.

THE LONGSHORE WATER SURFACE AS A FEEDING-GROUND FOR *G. PALPALIS*.

Number of each sex of *G. palpalis* and female percentage obtained on Maboko Island (*a*) by searching a path on the island, and (*b*) on a boat keeping pace, on two consecutive days in November 1932.

Date	Path on island			On boat, keeping pace		
	Male	Female	Female %	Male	Female	Female %
14.xi.32 . .	122	11	8	10	4	29
15.xi.32 . .	141	5	3	39	7	15

When attempting to account for the fact that some traps, in certain positions, speedily caught out the local flies, while others elsewhere continued to catch steadily small or large numbers, and others failed altogether, I was inclined to think, when I was on Maboko, that there existed (α) longshore flies, and (β) localised "to and fro" flies; that the former followed the water's edge, met with animals in and beside the water, not necessarily in one place every day, and found traps set on open banks and rocks at the edge of the water and on promontories. Having fed, these flies would land and rest in suitable thickets close by and might later continue in category (α) or might fall into category (β), this depending on how stationary were the animals on which they had fed. The "to and fro" flies (β) would be those which had discovered an animal that regularly frequented a spot or a path regularly traversed by man or animals, and had taken up their stations close by and so formed a "pocket" of fly. This might fill a trap for some days but would, as regards high numbers caught, soon come to an end. The neighbourhood of a good breeding-ground would also influence the numbers available.

(iii) *Riamugasire Island.*

(α) *Feeding-grounds on land.*

Areas resembling the feeding-haunts in Uganda were found in fact to be frequented by appreciably hungrier flies than areas equivalent to the

rest-haunts. The two sites were separated sometimes by as little as 12 or 15 yards. Activity seemed to go on rather later in the day, on both sides of the island, in the feeding-haunts (Jackson, Report, November 1932). Herbert Lloyd, in standing catches carried out (α) in a rest-haunt having a high canopy of fig trees, obtained lower hunger values than (β) in an open sandy patch flanking this rest-haunt, used by crocodiles for breeding and practically enclosed by thicket and papyrus, and (γ) a small sandy beach connected with (β) by a narrow opening; but the female percentages in (α) and (β) were on the average alike. In (γ) the female percentage was 20 as against from 12 to 14 in (α) and (β). Lloyd found that "The catch at the water's edge has a higher hunger stage and the female percentage is very appreciably higher. This is interesting in view of the fact that if a catch is made in a canoe the flies are hungrier and the female percentage is higher the further the catch is made from the shore."

(β) *Feeding-grounds over the water as revealed by canoe fly-catches.*

The earlier of the canoe fly catches were carried out by Lloyd in June 1934. "On the first two occasions on which these catches were made they were unaccompanied by any control catches on the shore. The flies taken were hungry and had high female and young percentages. Further, the proportion of old females was higher than in normal catches made on the shore. Owing to the formation of the island and semi-submerged rocks in the lake it was impossible to keep an even distance from the shore whilst the canoe circumnavigated the island. However, this brought out some interesting results. When catches made near the shore were compared with more distant ones, it became apparent that the further the flies were from the shore the hungrier they were and the higher were the young and female percentages. As one got nearer the shore the more common the flies became" (Lloyd, Report, July 1934).

Later catches were made with a parallel catch going on at the same time along the shore line. These were consistent in result with the previous canoe catches. The catches made on the shore were larger, had lower female and young percentages, and were less hungry than those taken in the canoe. The totals for this series were as follows :—

TABLE 18.

Catches of *G. palpalis* in a canoe compared with simultaneous longshore catches alongside.

Catch	Males	Females	Total	Female %	Young %	Mean hunger stage
Canoe . .	154	110	264	42	41	3·27
Shore . .	579	72	651	11	17	3·12

The differences between the two catches may have been due to one of two things :—either (*a*) the hungry flies are searching for food over water, or (*b*) the hungrier flies are following, or resting on, the shore, and were flying out from it to the canoe.

The difference in hunger is not very marked but the fact that the percentage of old females taken over the lake was thirteen times that of old females taken on shore affords very strong evidence in favour of the first explanation, for it is quite impossible that such a percentage should not have

been reflected on shore, if the flies had been resting or moving in the vegetation. Over the lake 156 old flies were taken and 38 of these (or 26%) were females. Over the shore 540 old flies were caught of which 10 only (or 1·8%) were females. The standard to take is definitely that of the old flies. The flies from the shore catch and the canoe catch were marked differentially. Three that had been marked on the shore were taken the same day in the canoe. Being hungry they may have gone to it either directly from the shore or, later, when food-flighting over the water.

Lloyd thought that, if the canoe catch were preceded a few minutes before by a catch on the shore or *vice versa*, the first catch might modify the character of the second catch, if the flies were merely flying out from shelter to the target of the canoe. If the second catch remained unmodified, the existence of two groups of flies would be suggested—one keeping on shore and another flighting over the water. These catches were made at a few minutes' interval. The first catch had in no case any apparent effect on the second catch. However, it was shown later that if a catch on the shore followed another catch on the shore, the sex ratios and the hunger of the two catches were practically identical. The results obtained by this last experiment, which was carried out three times, are given in the following table:—

TABLE 19.

Comparison of two successive catches of *G. palpalis* obtained in June along the longshore route referred to in Table 18.

Catch	Males	Females	Total	Female %	Young %	Mean hunger stage
1st . . .	1003	117	1120	10	17	3·11
2nd . . .	596	71	667	11	17	3·09

The flies were marked differentially and of the 667 flies taken in the second catch only four had been taken in the first catch. These were two young females and two stage iii * males. That the two catches on the shore should be so alike in consistency and that so few of the same individuals figured in both, would, in a place in which the flies are confined within a small area, have seemed strange, if it had not been for Fiske's ample proof that the shore population is a moving one. This experiment affords further evidence of that fact.

The addition to the above of "successive" shore experiments in July gave the following combined totals for all:—

TABLE 20.

COMPARISON OF SUCCESSIVE CATCHES OF *G. PALPALIS* OBTAINED ALONG THE LONGSHORE ROUTE REFERRED TO IN TABLES 18 AND 19.

Totals of first and second catches respectively for the months of June and July combined.

Catch	Males	Females	Total	Female %	Young %	Old female %	Mean hunger stage
1st . .	1933	225	2158	10	17	20	3·09
2nd . .	1122	178	1300	13	20	29	3·11

* See p. 38.

One further canoe catch was carried out in July, in which month the density, hunger, and female and young percentages, had all decreased as against those of June. This catch followed the old canoe course and was preceded by a catch round the margin of the island five minutes before in which a blanket screen was used for the special attraction of female flies. The hunger and female and young percentages still remained higher in the canoe than on land.

Feeding-grounds over the water are evidenced from standing catches on rocks in the lake near the shore. These catches were carried out by Lloyd on two different rocks, both of which normally provided crocodiles with basking amenities. They were separated from the dry land by a belt of papyrus about ten yards wide. This papyrus also screened the catching party from the shore so that no flies were attracted out from the shore to it. Unfortunately a really ideal site could not be found. The disadvantage of this one was that, though the party itself was shielded from the fly on the shore, there were some rocks to the side of the catching rocks which were in full sight of fly bush on the shore. It was possible for flies on the shore to see these rocks and fly to them and thence across to the catching party. One of the two rocks used was right against the papyrus and the other was separated from it by two yards of water. The catches are summarised in the following table :—

TABLE 21.

Comparison of the composition of simultaneous catches of *G. palpalis* (*a*) on rocks in Lake Victoria, and (*b*) on the adjacent shore.

Catch	Males	Females	Total	Female %	Old female percentage of female catch	Young %	Mean hunger stage
Rock . .	109	41	150	27	60	27	3·39
Shore . .	322	35	357	10	13	10	3·12

As in the canoe catches, the catch over the water shows higher hunger and higher percentages of old females and young than the catch over the shore.

Actually, on land on Riamugasire, old female flies were comparatively seldom met with at man, the percentage of old females of all the old flies collected on all the fly rounds in two years being only about 7. On crocodiles, as on the rocks and canoe, it is very different. On one occasion four gorged old female flies were taken from a place from which a crocodile had just been seen to move off; they were found to contain nucleated, oval blood corpuscles. On another occasion the following flies were taken off a shot crocodile; 7 old females, 3 young females, 7 males of stage iv (hungry), and 2 males of stage iii.*

(e) The evidence from the fly round and standing catches on Riamugasire Island on the effect of different vegetational communities on the density, condition, and composition of a population of *G. palpalis*.

This long narrow island possesses for practical purposes two sides only †—a west side (sections 3–1, 9 and 10) and an east side (sections 5 and 6). Between the greater part of these two margins is the homogeneous dry thicket. The vegetation types of the margins occur mixed in fragments too small to

* See p. 38 and pl. 21. † See fig. 12 on p. 129.

give clear-cut results in all cases, through the proximity of feeding and rest-haunts, but at least the more extensive of them have responded to our fly rounds and stationary catches.

The fly round had twelve sections and was 3,240 yards in length. It passes round the island, tapping each vegetational type at least twice, and it was carried out alternately—once forwards and once backwards—to cancel out time of day, from April 1933 to November 1934. The flies were marked, not killed, so that information might be obtained from recaptures and the population remain unreduced. A number of population-estimation experiments were carried out also, using marking and the " recovery index " (see p. 36 above and appendix 3).

The following, broadly, was the result as regards the relation of the flies to the vegetational types.

(i) *Unbroken dry thicket (four sections).*

Flies and pupae rare and female percentages high, but the males unexpectedly replete.

(ii) *Cultivation.*

Between April 1933 and November 1934 only 11 (7 males and 4 females) flies were taken in cultivation (section 12)—all in the first three months. The mean hunger stage was 3·40 (quite high), density per 100 yards for the three months 0·2, female percentage 36·4, female percentage of old flies only 28·6, and the percentage of young flies 36·4. The female and young percentages were thus far higher than anywhere else and (so far as the small figures permit) confirmed the view that unfavourable country is penetrated by hungry flies only.

(iii) *Sections with good interspersal.*

In the following table the sections are grouped in order of hunger. The word " Crocodiles " denotes the presence of regular crocodile basking-places.

TABLE 22.

Density, composition, and condition of the population of *G. palpalis*, on some sections of the Riamugasire fly round.

Section no.	Length of section in yards	Character of section	Wind averages during observations, in feet per second	Mean hunger stage	Density per 100 yards	Female %	Young %	Female % of old flies
6	333	Water's edge	290	3·33	9·4	20·3	24·2	7·4
9	315	Rocks, fig canopy, crocodiles	203	3·26	6·0	15·4	18·7	6·1
5	526	Water, crocodiles, thicket	201	3·25	14·0	15·5	19·2	5·5
3	83	Crocodiles and thicket	118	3·25	23·8	9·7	13·2	3·2
1	283	Mixed	111	3·23	9·3	12·7	18·1	8·7
2	90	Rocks, high fig canopy	54	3·23	26·3	8·2	10·8	2·9
10	160	Similar to section 5	94	3·22	11·35	14·2	15·2	6·2

It is noticeable in this table that hunger approximately follows wind values and that low female percentage coincides with high density, except in the very mixed section 1. As regards density, section 2 (high fig canopy over open rocks, undergrowth light) and section 3 (crocodile basking-place bordered with umbrella thicket) show throughout the whole period (April 1933 to November 1934) by far the highest density combined with the lowest female percentage (in old flies considered alone) of all these sections, section 2 having the fewest females of all. Both show far higher hunger from April to June and lower hunger thereafter. Next in order of density come 5 (water, crocodiles' basking-places, a little thicket), 10 (in character like 5) and 6 (water's edge); with 6 ranks the section with the most mingled interspersal, namely 1; 9 comes last.

Sections 1 and 6 show the highest, and sections 10 and 9 nearly as high, female percentage in old flies considered alone; section 5 follows close. But generally the order in these respects is the reverse of that of the density. These sections all are (or contain) probable feeding-grounds—a fact that is brought out still better when the hungrier flies only are considered. The percentage of young flies is highest along the water's edge in section 6, which also shows highest wind, highest hunger and highest general (as opposed to old) female percentage.

The catches in section 2, the rest-haunt *par excellence* of the island (unless final consideration of the standing catch results should oppose this description), supported the view that the male flies seeking females tend to linger in greatest numbers in the best sheltered spots. A part of section 3 passed through very well-sheltered bush of the section 2 type, and the flies from this seemingly influenced the result more than those of the basking-ground. Even here the elimination of the unhungry males gives section 3 something of a feeding-ground character. Section 9 (canopy of large figs over rocks, crocodiles basking on the lower parts, where also some thicket is present) shows a far lower density than section 2, also with the fig canopy and rocks, somewhat higher hunger and a markedly higher female proportion, especially after June 1933, and is evidently more of a feeding-ground.

Section 1 passed through very open crocodile basking-grounds, thorny thickets with *Euphorbia Tirucalli* and *Sanseviera*, lighter thickets and rocks supporting candelabra euphorbias, aloes and fig trees.

It will be seen from the above and from what follows that throughout the work few old females were coming to man, though their numbers varied with month and place, and that the female percentage was everywhere heavily masked by the presence of males out for mating; and that, generally, spots and stretches of rest-haunt character still showed highest density, lowest hunger and fewest females appearing, while the water margins and the sections with many crocodile basking-places showed on the whole lower density, higher hunger and higher female percentage. Open cultivation and close homogeneous thicket both seemed repulsive to the flies, but those found in the former were hungry and in both the female percentage was high. Differential conditions on each side of the island also exercised a strong influence, as is noted below.

(f) Summary as regards the use of the habitat parts and the incentive governing it. *

(i) *Rest-haunts.*

At the close of each period of activity each sex re-seeks massive shelter.

* Adapted from Fiske (1920).

(ii) *Feeding-grounds.*

Stimulus—recurrent hunger. Every second or third day (this being the apparent hunger-cycle in *G. palpalis*) both sexes, if food has not appeared in the rest-haunt, make food-hunting flights along lake and river margins and those of open spaces.

(iii) *Breeding-grounds.*

Stimulus—maternal instinct. At intervals of eight days or longer the females seek the breeding-grounds : often lighter woody shelter than is used for the rest-haunt, though the latter is in some cases used also.

(iv) *Assembling-grounds.*

Stimulus—masculine instinct. Methods followed :—

(α) *Haunting of the routes along which females must pass.*

Daily the males leave shelter and undertake " assembling " flights to and along places where the females may congregate or pass. These places may be the feeding-grounds if shelter be present.

(β) *The following swarm.*

In *G. palpalis,* following swarms do not form on man, sheep, or goat, these being less-favoured hosts, but do form on crocodile, monitor lizard, tortoise, hippopotamus, and situtunga, the male flies attracted to these animals being inclined not to pass on, but to linger indefinitely. They do not transfer to man when, through inactivity of the animals (in the case of the tortoise) or his own stealth or shooting, he comes up to them, but on the contrary, disperse. The object is the meeting of the sexes.

5.—THE EFFECT OF PHYSICAL FACTORS.

(a) The elevational and geological habitats as indicators of the general climate.

Lake Victoria lies at 3,720 feet; *G. palpalis* is recorded as occurring at 4,600 feet in Angola, 5,300 feet in Katanga, Belgian Congo, and above 5,000 feet in the Kivu volcanoes (Newstead, 1924 : 142). The last two records apply to the east African subspecies *fuscipes.* The latter occurs at the level of Lake Tanganyika (2,550 feet) and of Lake Rudolph (1,230 feet, as given by Champion, 1935), but typical *G. palpalis* occurs on the West Coast down to sea-level. The species, as we know from our own observations, changes its habits in detail with varying temperature and humidity, but obviously, like *G. morsitans* and *G. pallidipes*, it can support a wide range of general climate, particularly as regards temperature and pressure. Its range is as catholic as that of *G. pallidipes.* All that probably matters is that it should have available sufficiently shady, close shelter with nooks giving high humidity in addition to feeding facilities.

(b) The object of the investigations.

Fiske and Carpenter, each in the course of observations on *G. palpalis* in a very great number of places, found a regular correlation between a high female percentage and (i) general lack of food animals, (ii) unshady vegetative types, which only hungry flies searching for food would enter. Greatest density, but not necessarily high female percentage, was found at spots haunted regularly by the food animals preferred by the fly. On the other hand, on extending his observations to the marginal surface of the lake, at a spot where the

female percentage on land was not high, Fiske at once obtained a very high female percentage, as Herbert Lloyd has done since consistently in his rock and canoe experiments (see pp. 139 and 141 above). Also, even where the percentage was not specially high, Fiske found by means of numberless standing catches that a movement was all the time taking place—whether along lake-shore or the contact of woodland and open—that would have shown a very high female percentage if this had not been masked by the presence of "loitering males." Continual movement was thus associated with the females especially.

Our own work on *G. palpalis* has confirmed this. Further, working extensively on *G. morsitans* and *G. swynnertoni*, we found that they also had rest-haunts and that they also left these when hungry. They, again, searched the contacts of woodland and open where such contacts were provided, in their case by glade and mbuga; and we found preponderance of females in country unattractive to the species. We called our woodland-with-open-ground contacts, corresponding to the water-margin and open-ground-margins of *G. palpalis*, "feeding-grounds"—which is what they were; and we proved that the flies resorted to them when hungry; but unlike Fiske, we were able to correlate the hunger of the flies, not with seasonal presence and absence of food animals—for very few of these seemed to suffice—but with high atmospheric dryness. We wished to ascertain for *G. palpalis* also whether physical factors, modifiable through the vegetation, produced hunger and reduction of density. A meteorological station was erected (as stated already) on the west side of Riamugasire Island, with a thermohygrograph, an atmometer, a rain-gauge and an anemometer; and the results of the fly rounds and other observations and catches were correlated with the readings.

(c) The effect of temperature and humidity on *G. palpalis* in Uganda.

Carpenter has stated (1920 : 42) that "the drier months of the year cause a large falling off in numbers" and speaks of "the trying period of diminished humidity." He gives a graph which shows a perfect correlation between rise of relative humidity, fall of temperature, rise of fly density, and rise of female percentage—and their opposites. The figures were obtained at Jinja on the mainland, where from the beginning of August to the end of January the relative humidity varied from 63% to 76%. On Bugala Isle no such relationship could be made out, but there the relative humidity varied only from 77% to 72% during a continuous period of 12 months. "Probably . . . the humidity of the atmosphere was so much more constant on the island that a higher temperature did not necessarily kill off the flies. . . . Secondly, the hunger of the females, as estimated by the number caught, is very dependent upon the temperature." The hotter the month, the day, and the hour, the less the fly bites.

(d) The daily routine of the weather and fly behaviour on Riamugasire Island.

"In order to get a more intimate contact with the fly than could be given by the routine rounds, 'drift' experiments were carried out by stationary catchers at eight points on the island. They were used to test the drift of the flies through various sites during the hours of the day. In every case one party of the catchers operated in the rest-haunt and another in the feeding-haunt, both parties remaining stationary for, usually, about 6 hours. Flies were recorded (sex, hunger, and whether young or not) in quarter-hour periods :

at the end of every period various instruments were read. The two sides of the island gave different results" (Jackson, who considers, however, that the figures obtained require fuller examination).

Most of these drift experiments took place on the east (the landward) side of the island, "where the following conditions were found to be customary. In the early morning (before about 8 a.m.) it was cold and damp, with a breeze of varying strength blowing from the land. Subsequently temperature rose rather suddenly; saturation deficit rose. About 10 o'clock temperature rose to a high figure which was maintained for some hours. Subsequently, on sunny days, but not necessarily on dull ones, the wind dropped, and saturation deficit rose rather sharply, although temperature was much the same. The breeze then turned (about 11.30), now blowing strongly from the west off the lake. But the east side of the island, being sheltered from the lake breeze, showed no appreciable change in temperature, saturation deficit, or wind force, which last remained very low. This condition continued into the afternoon, when, about 2 or 3 o'clock, temperature and saturation deficit both began to fall, reaching a low level by 5 p.m.

"It was observed that fly became active with the rising temperature at about 74 degrees in the early morning, and that it became maximally active at about 77 or 78 degrees. This activity continued until the rise in the saturation deficit a little before the wind changed, when activity became less, and remained fairly low until the saturation deficit fell in the afternoon. There was then some slight resumption of activity, which was soon cut short by falling temperature. On a dull day, when conditions were more humid, and the saturation deficit failed to rise before the wind changed, the mid-morning activity was continued evenly into the afternoon.

"On the west side of the island, activity very greatly diminishes, almost ceasing in the 'rest-haunt,' as soon as the wind changes from a land to a lake (west) breeze. The flies inhabiting this side of the island, owing to the marked fall in temperature associated with the change of wind [and, see below, rise in humidity], have far less hours of the day in which to be active than have those on the east side" (Jackson, November 1933).

Mean temperature and hunger were both high on the east (land) side of the island and low on the west side (lake wind). Quite hungry flies could be got on the west side also, *but in feeding-haunts*. Feeding- and rest-haunts, not shown on the fly round, were revealed by the standing catches both on Riamugasire and on the mainland and, loitering males being eliminated, showed something like the female percentages that the mean hunger stages suggested.

Jackson suggested from the data:—(i) that it is likely that there is an optimal temperature for fly activity at about 79° F., perhaps provided that the saturation deficit does not exceed 0·40 inches; but that (ii) it is possible that, from the time when a naked black bulb thermometer reaches 110° F. in the sun, activity is largely inhibited for the rest of the day, whatever conditions may supervene; and that (iii) high winds also inhibit activity.

(e) The evidence of the round of the seasons.

(i) *Density, composition, and condition of the population of* G. palpalis, *appearing to man.*

The following tables give the density, composition, and condition of *G. palpalis* appearing to man over various periods and the mean meteorological readings during those periods.

TABLE 23.

Density, composition, and condition of the population of *G. palpalis*, appearing to man, and the mean meteorological readings during the period from April 1933 to March 1934.

Month	Old males per round	Mean hunger stage	Young flies per round	Young fly %	Old females per round	Old females %	Females appearing %
April	350	3·71	163	29	44	8	12·5
May	·272	3·56	98	26	17	5	6·6
June	183	3·53	82	30	4	1	2·2
July	150	3·30	36	19	2	1	1·3
August	143	3·32	17	11	2	1	1·3
September	94	3·20	20	17	3	3	3·2
October	93	3·10	26	21	5	4	5·3
November	110	3·13	17	13	4	3	3·7
December	104	3·16	16	13	3	2	2·8
January	171	3·14	39	18	6	3	3·7
February	175	3·28	48	21	7	3	4·3
March	140	3·28	28	16	6	3	3·7

Old female deficit, or, conversely, as above, old female percentage appearing, is calculated on the estimated old female population, assuming it to be the same as the male.

Month	Mean daily temperature	Relative humidity	Absolute humidity	Saturation deficit	Wind	Evaporation *	Rain	Sun
April	75·9	81	0·732	0·139	64	38	1·43	—
May	74·7	89	0·757	0·109	47	28	3·51	—
June	74·1	87	0·732	0·106	59	39	1·35	8·98
July	72·8	83	0·661	0·149	54	36	0·20	8·63
August	69·4	80	0·555	0·132	—	35	1·27	7·65
September	72·8	69	0·555	0·255	64	42	0·28	8·21
October	73·2	73	0·595	0·215	60	35	1·75	8·38
November	73·3	71	0·575	0·235	51	28	1·18	8·53
December	71·4	80	0·616	0·141	24	21	3·85	7·35
January	72·8	77	0·616	0·194	32	25	0·29	7·41
February	72·4	63	0·575	0·208	45	30	0·77	8·46
March	72·6	77	0·616	0·194	47	29	1·05	7·70

* White bulb at four feet, Livingston atmometer.

TABLE 24.

The data contained in Table 23 continued for the period from April to November 1934.

Month	Old males per round	Mean hunger stage	Young fly per round	Young fly %	Old females per round	Old female %
April	148	3·12	28	15	14	9
May	174	3·19	8	4	16	8
June	155	3·16	47	22	7	4
July	156	3·11	36	18	7	4
August	103	3·15	23	17	4	4
September	81	3·29	14	14	5	6
October	81	3·19	21	19	6	7
November	81	3·13	11	12	6	7

TABLE 24.—*continued.*

Month	Mean daily temperature	Relative humidity	Absolute humidity	Saturation deficit	Wind	Evaporation	Rain	Sun
April .	72·4	80	0·638	0·145	60	24	4·85	6·2
May .	72·5	77	0·595	0·188	17	19	3·83	7·8
June .	74·1	75	0·638	0·200	23	27	0·12	8·5
July .	73·5	71	0·575	0·235	31	28	0·25	8·3
August .	73·7	67	0·555	0·273	39	30	0·62	7·9
September	75·2	64	0·555	0·311	46	36	0·15	8·2
October .	74·3	71	0·595	0·233	47	29	2·71	7·3
November.	75·0	75	0·661	0·205	44	25	0·51	7·7

In a normal year the rainfall at Musoma is as follows :-

TABLE 25.

Average monthly rainfall at Musoma.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1·9	1·1	3·9	5·1	4·0	0·5	0·8	1·1	1·1	1·6	1·2	3·5

Total rainfall = 25·8 inches.

Thus in 1933 the months of May, June, July, August, October, November, and December had normal rains. The months of April, September, January, February, and March were abnormally dry. In 1934 the departures from normal were small.

Taking other factors into account, April 1933 can be characterised as hot and fairly dry; May as warm and wet; June as cooler and fairly dry; July as cool and dry; August cool and damp; September to November warm and dry, September driest; December cooler and wet. In 1934 the months January to March showed moderate temperature and were fairly dry; April and May moderate temperatures and wet; June and July warm and dry; August warm and fairly dry; September hot and dry; October warm and damp; November warm and fairly dry.

(ii) *The seasonal changes in the density, composition, condition, and activities of the fly population.*

(α) *General activity density.*

The fly numbers appearing to man did not rise in April 1934 to anything like the height at which they stood a year before. From April 1933, a hot dry month, followed by two months hardly less hot, but with a much lowered saturation deficit, there was a heavy and steady fall to a minimum fly density in the period from September to December. There was then a rise in January and February 1934. Thereafter numbers dropped slightly and remained steady until August, when (with September, hot and dry) there was a further fall to a new minimum level in October and November. This minimum was even lower than that of the preceding year.

(β) *Estimated true density.*

This was determined from the "recovery index" (see p. 36 above and appendix 3). In April 1933 the estimated figure was 22,000 males—

quite definitely between 16,000 and 27,000. In May there was a fall to about 12,500—certainly between 11,000 and 15,000. In June and in all succeeding months it was estimated that true density was in the neighbourhood of 5,000 with a possible error of about 1,500 above and below this figure. Recaptures were too few for closer estimations than these to be made in the various months.

(γ) *Number of pupae.*

As in Uganda, so on Riamugasire Island, live pupae seemed to be more numerous in dry weather, when flies were apparently least numerous.

(δ) *Emergence.*

The young flies were observed in two periods—one averaging 28 per round from April to June, and a second, averaging 16·5 during the remaining 9 months of the year. This fits the temperature; it also shows broadly an inverse relation to saturation deficit and to the rate of larviposition. A high number of young flies on the round and high young fly percentage correspond with periods of high density or incipient decrease. Their numbers agree roughly, even to minor variations, with the number of hungry flies.

(ε) *Hunger and food.*

The curve of the mean hunger stage follows generally the apparent density curve. It will be noted (in the table above) that the hunger figures are the opposite of what we find in *G. morsitans*, being higher the lower the saturation deficit or the higher the humidity; and that the females behave in agreement. The crocodiles, present continuously from the beginning of the period, became most numerous from June to August. The peak was reached in July 1933 (Lloyd) when about fifty were counted on the main island and the islets. From September they diminished, and by December there were none on Riamugasire Island. In 1934 they were numerous from June to September.

(ζ) *Longevity.*

Jackson calculated from the recaptures of marked flies that males of *G. palpalis* on the average did not live more than seven weeks on Riamugasire Island; of the flies marked on the rounds from April to June 1933 none were recaptured after 60 days and only 8 after 40. Of the far smaller numbers marked from July to December, despite lesser density and fewer fly rounds, 15 were recaptured after 40 days and one after 73. Females of *G. morsitans* live longer than males in the field, and this is probably true also of *G. palpalis*. This does not mean that an occasional male may not live for a long time. Carpenter's recaptures of a male of *G. palpalis* after 247–253 days and a female after 182 days may be noted here.

(iii) *Discussion of seasonal changes in density.*

" While it is evident that both hunger and numbers appearing to man show a broad correlation with either temperature (particularly higher temperatures) or absolute humidity, the agreements are not very close. Thus hunger and high apparent density seem to be associated with hot or with warm and damp conditions. The young fly percentage seems to agree best with temperature.

" The estimates of true density (population) do not, however, support the view that periods when the flies are hungrier are those when flies are more inclined to show themselves to the catchers. Thus the ratio of apparent density

to true density appears no higher in April, May, and June, when hunger was high, than at any other time. It would therefore appear (*a*) that hunger does *not* enhance activity, and (*b*) that activity does *not* cause hunger.

"Yet it seems that hunger *must* cause increased activity of young flies. These are found in proportions which must be greater than their true proportion in the field, and it is a reasonable assumption that this may be due to hunger.

"It *might* be suggested that at hungry periods the more replete males conceal themselves for some reason and so nullify the effect of the greater activity of hungrier individuals. Of this, however, there is no evidence whatever.

"Further, why do numbers [appearing] and true density both fall through the dry months, September to November, while apparently longevity is greater, hunger less, and breeding proceeds freely?" (Jackson).

Jackson, convinced from all the results that high temperature produces hunger, suggested that from April to July the changes in density are best associated with the daily mean temperature, and from then on (possibly) with absolute humidity. But despite a minimum mean temperature in August, the fall continued to a minimum in September. However, if we divide the year broadly into three periods—that in which something is causing a heavy fall in density (April to August), that of the actual "trough," and that of the marked new rise (January to March), we find a negative correlation between density and saturation deficit and a positive correlation with humidity.

TABLE 26.

A possible relation, in certain periods, between saturation deficit and the density of *G. palpalis*.

	Temperature	Saturation deficit	Relative hum.	Absolute hum.	Evaporation	Old males per round	Old females per round	Mean hunger stage
1933/34								
April–August	73·4	0·127	84	0·687	35	220	14	3·54
September–November	73·1	0·235	71	0·575	35	100	4	3·15
December–March	72·3	0·184	74	0·605	26	162	6	3·23
April–August	73·2	0·194	74	0·600	26	147	10	3·15
September–November	74·7	0·250	70	0·604	30	81	6	3·20

Actually, here, the mid-period for the density and hunger figures has been taken as September to November to allow for a possible lag.

It does not work out fully in detail. Turning back to tables 23 and 24, we find that a big drop apparently followed a fairly high saturation deficit in April 1933, but that the fall continued strongly during June and July despite a low saturation deficiency in May and June. High saturation deficiency from July to November—the peak in September, and very high in October–November—witnessed a fall to the minimum activity-density of 1933 in the four months September–December. In December the saturation deficit fell greatly and in January the fly numbers rose. They remained fairly steady in February and March with the saturation deficit once again high for January–February–March. A rise in activity-density in May followed a lowering of the saturation deficit in April, a small fall of the former in June–July was accompanied by a rise in the latter. The deficiency reached a peak in August and the fly numbers

dropped to their minimum for 1934 in the months September–November. There were no observations after that date.

In May and June 1934, though the saturation deficit was low, the temperature continued high, but in September the possible inference that both high saturation deficit and high temperature *per se* may affect the flies adversely is perhaps rather negatived by the relative steadiness of the fly population in the period January to March.

Also, as stated already, the breeding seemed good, the hunger was less and longevity (of males—in Jackson's recoveries) was apparently greater during the dry period September–November. How then did heightened saturation deficit or temperature—both regarded by Carpenter as well as ourselves as, probably, the lethal factors—kill off the flies, if either did so? This question is difficult to answer. Jackson suggested in a letter (25.iv.35) that the young flies, which must find food rapidly in order to survive and so must face unfavourable conditions, may have been killed off almost at birth by high saturation deficit. The young fly numbers roughly followed the density figures. Did the latter fall because the young flies were being killed or the young fly production fall because something else was reducing the density? The young flies came to the catchers in a proportion which must have been greater than their actual proportion in the field, and it is a reasonable assumption that this must have been due to hunger. It is noteworthy that the female percentage appearing to man, though it fell as the crocodiles reached their peak in August 1933, and (less so) when they reached their next peak in June and September 1934, did not rise at all high when the crocodiles left the island. All the factors referred to in the tables above have been thought out very fully in relation to the falls and rises in the fly population. The result has been inconclusive through the association of lessened hunger with the factors (saturation deficit and temperature) which seemed associated with falls in fly density; but it has been felt that a further examination of the mass of data accumulated might yet give us the reply and that laboratory tests certainly would do so. Carpenter's conclusions from his meteorological observations in Uganda (1913 : 11) may at this point be recalled :—

"1. Decreased relative humidity is unfavourable to the adult fly.
2. Higher temperatures are particularly unfavourable to the female sex.
3. There is an inverse relation between relative humidity and rate of larviposition."

In connection with "3" above, p. 188 should be consulted. Nos. "1" and "2," above, though confirmatory, do not help us further, unless such factors as desiccation and heat are capable of destroying the flies (despite availability of cover) without first making them hungry or bringing females in larger numbers to man.

It was, actually, highly unfortunate that through shortage of staff our investigations had to be closed (temporarily, I very much hope) before the explanation was confirmed or laboratory tests carried out. Mr. K. Mellanby's visit to Entebbe meantime especially to carry out such tests is very heartily welcomed.

(iv) *The effect of rain on* G. palpalis.

Moggridge pointed out that a peak period of apparent activity–density corresponded with a period of heavy rainfall during the month of May. According to him also, the minor rises in density seemed to take place immediately after rain and the degree of increase seemed to be influenced by the amount of the

precipitation. Koch, in his catching-out experiment on Riamugasire, made the same observation, and Chorley has made it for Uganda. It does not, however, seem to be borne out by the Riamugasire observations as a whole. A graph of Carpenter's (1912 : 84) shows the opposite—a strongly marked negative correlation between rainfall and fly numbers which may be partly an activity effect.

(v) *The effect of wind.*

(α) *Recapitulation of the daily routine of the wind.*

The wind appeared to be something of a master factor. On Riamugasire the wind blows in two directions each day. As stated already, till the land mass has become heated up it blows strongly towards the warmer open lake, that is to say, in a westerly direction. As the land warms up the wind gradually drops and, after a slight lull, suddenly blows strongly from the lake to the now much hotter land mass, *i.e.* in an easterly direction. When the land cools down at night, the wind gradually drops (at about 8 p.m.) and then rises from the east again.

Our meteorological station on Riamugasire, being on the western side of the island, was sheltered from the morning wind, and the temperature was little affected by the latter, though humidity gradually diminished. But when the stronger wind suddenly rose from the west each day, blowing from over the damp lake, there was an immediate drop in the temperature amounting to from six to ten degrees, and this was accompanied by a rise in relative humidity of as much as from 10 to 15%. The wind might spring from the west between 11 a.m. and 3 p.m., this depending on how quickly the land warmed up, owing to the presence or absence of cloud.

(β) *The effect of wind on the flies.*

The numbers of flies appearing to the catchers is in a large proportion of instances in inverse ratio to the velocity of the wind at the time of the catch. May 8th–10th, January 25th–27th, and February 12th–13th were peak catches as regards numbers, and on these catches minimum wind velocities were registered.

The transects of the fly round with higher wind force produced the hungriest flies; and experiments of Lloyd's on land, in which he compared the hunger of flies coming to man in winds ranging from 54 to 290 feet per minute, led him to the conclusion that the higher winds cause the non-hungry flies to remain in the vegetation. The effect of the wind was, however, probably more than merely mechanical; for Moggridge showed that the rises and falls in fly numbers on the western side of the island occurred inversely to the rises and falls of the relative humidity; and this, we have seen, rose with the wind from the west. There was not the same correlation with humidity on the east side of the island, but there, when the wind blew in force, the fly catches were small, and *vice versa*; perhaps these were mechanical effects. The wind sometimes reached 12 miles an hour.

(γ) *Rock catches by Lloyd to test the effect of wind of different velocities on the activity of feeding flies.*

The "rock" catches referred to on p. 141 above were carried out on the west side of the island. In this way they were sheltered from the morning breeze and received the full force of the afternoon breeze. During these particular catches no flies were taken after the wind, having changed, had attained its maximum force. It was therefore thought that flies might not

move over the water or out from the shore against the wind except towards moving objects. Flies had already been taken in canoes in full view of the shore when a strong wind was blowing towards the shore. These catches were therefore designed to see whether flies would visit rocks in the water in full force of the wind. The catches were carried out on one of the rocks already mentioned. One party çaught on the rock while a control party caught on the island behind the fringing papyrus. Two catches were carried out, each of which may be divided into three periods :—(i) when the wind was blowing from the east—when practically no wind is felt on the rock, this period including also a complete lull in the wind while its direction was changing; (ii) when the wind was blowing from the west but was not yet exceeding two miles an hour, this period lasting from an hour to an hour and a half; and (iii) when the wind was blowing strongly from the west at a speed of seven or eight miles an hour. The start and end of period (ii) is strongly marked. The approaching wind is indicated by a line on the lake which marks the edge of the rougher water. The stronger wind rises suddenly and the increase in velocity is rapid.

Flies were taken on the rock after the wind had thus increased in velocity, showing that some of them will brave it. The ratio of the rock catch to the control catch during the three periods was, however, as follows :—

Nature of catch.	Rock catch.	Control catch.
Period (i)	1	1·85
Period (ii)	1	2·03
Period (iii)	1	7·67

The activity of flies on dry land is reduced by a strong wind, but it can be seen from the figures that this effect is more marked in flies travelling over water. They show also that wind of a velocity up to two miles an hour has little effect. Crocodiles basking on rocks which are slightly submerged, or which only just jut out of the water, move off from these sites as soon as the waves become more than ripples, thus robbing the fly of part of its food supply in any case on the advent of wind. But crocodiles on rocks that are well out of the water remain there, so that it is doubtless not coincident disappearance of food but actual dislike of the wind that reduces the activity of the flies.

(vi) *The effect of cloud.*

C. W. Chorley has established an interesting correlation between the behaviour of the flies and the weather indications afforded by the different categories of cloud. Traps catch better on days of wool-pack cloud than on days of unmitigated sun. As regards general cloudiness the observation * is given that " when clouds cover the sun, flies spread all over the island, even to the grassy tops, and are more ready to feed."

The details, condensed, are as follows :—

Cirro-cumulus clouds (mackerel sky). Flies are most persistent and inquisitive from 8 to 11 a.m. They investigate any strange object, are not interested in feeding but (males) merely want females, they move round the object investigated in half-hoop flights, and the male percentage, whether taken by screen or by hand, is usually very high. The male percentage is higher than female in crinoline-form traps.

Cumulus or strato-cumulus clouds (wool-pack). Flies are most active, males and females leave their rest-haunts and travel great distances irrespective of type of country, over as much as 300 yards of clearing, across open spaces of

* This observation was made on the Sesse Islands.

water and along the fringe of papyrus beds—noted for as much as two miles. On such days of clear visibility every type of foreshore vegetation yields flies and the density at man is very high. Large catches of both sexes are made in crinoline-form traps.

Cirro-alto-cumulus clouds (denoting fine windy weather). Both sexes are very eager to bite in the early hours and in the late evening, but very few do so from 10 a.m. to 4 or 5 p.m. Their range is restricted to their regular routes. Crinoline-form traps catch during the early and late hours only and males exceed females.

Cumulus nimbus (thunder clouds). Before the wind of an oncoming storm males and females attack in large numbers and very persistently, probing without delay. They do not select the shady side of objects attacked, as at other times. They remain on an inanimate object for as much as from 20 minutes to half an hour, searching and probing, before giving up the attempt. Density of both sexes is very high both at catchers and catching screen just before a storm. The traps catch more females than males.

Heavy overcast sky, low clouds, misty or raining. Flies are inactive even in heavily infested sites and might often be imagined to be absent. Crinoline traps catch few or no flies.

Overcast sky due to heat haze. Flies are not active; a few are eager to feed early in the day and towards evening but the apparent density is very low and catching, whether by hand or by screen, gives fallacious results, the latter being far too low. Crinoline-form traps catch few flies at morning and evening, but more in the middle of the day.

Clear, cloudless sky, bright sun, no wind. After rain in the night or early morning flies of both sexes are eager to feed " so long as the moist atmosphere holds the pungent smell of vegetation." Fair catches of both sexes by hand and screen. Crinoline traps catch a high percentage of females in this weather after rain.

Clear, cloudless sky, bright sun, but a strong breeze. Flies of either sex are inclined to feed only in the morning and evening, when the breeze is lighter. Crinoline traps catch both sexes in small numbers, also at these times only.

6.—TWO MAINLAND LOCALITIES.

(a) A lake-shore locality, near Musoma, on the south shore of Mara Bay.

Limited longshore strips of *G. palpalis* and *G. brevipalpis* exist at, and near, Nyabangi, east of Musoma. Two rounds—those of Bugya (east) and Bweli (west)—were carried out here fourteen times as a slight but possibly valuable check on the work on Riamugasire Island, which is not far away. It was impossible to spare meteorological instruments for these mainland rounds, but a whirling hygrometer and anemometer (Biram Air-meter) were carried to assist in the analysis of the activity of the flies.

(i) *Bugya.*

Low closed wooding and thicket, backed by a rocky granite hill and fronted by reeds, formed the centre. On either flank was *Acacia spirocarpa* savanna fronted by ambatch. There were two sections only and they showed very similar results. In the *spirocarpa* savannas were impala, dikdik, greater kudu. In the kopje and dense wooding there were also baboons and monkeys, on the water-front monitor lizards, crocodiles, and water-birds.

The main piece of information obtained was that the fly density

differed seasonally from that of Riamugasire. It was minimal in February, when the round started, and rose till the end of July, when it started to decrease again. " It is possible that a peak catch might have been registered in June if a round had been done during that month " (Lloyd).

(ii) *Bweli* (*West Nyabangi*).

As seen from the fjord, enumerating from east to west, this locality consists (α) of a considerable ambatch frontage, extending yet further eastward; (β) westward an old overgrown garden and orchard including a small grove of mangoes, just in front of which is a break in the ambatch and a rock close inshore where a crocodile lies; (γ) a low, long granite kopje, well bushed and treed, the large squarish rocks merely showing amongst dark vegetation; (δ) a low shelf back from the water with *A. spirocarpa* trees, ambatch in front of them, and a kopje behind the shelf; (ε) a further less-clothed granite kopje; (η) 100 yards of open grass, with *spirocarpa* savanna at the back; (θ) a bay bending back and containing papyrus and ambatch. On the land open grass with *spirocarpa* savanna and an odd village behind.

The fauna includes bushbuck, dikdik, baboons, monkeys, crocodiles, monitor lizards, and the usual water-birds.

The rounds showed the following vegetational divisions :—

(α) beach generally; (with one exception (no. 3), in which however only 14 males were taken, the beach transects were the hungriest and also (including 3) showed the highest female percentage; there was little shelter on the beaches for loitering males).

(β) damp thicket, with more shelter for loitering males so that hunger was lower;

(γ) mangoes; (ideal for loitering males so that hunger was yet lower).

(δ) dry thicket on the side of the hill; (evidently unfavourable, as on Riamugasire Island, density being very low (8 flies altogether) and hunger low also).

The seasonal density of the flies differed completely from that on the island and to some extent from that of the Bugya round. " Instead of a progressive rise in numbers during January and February, we find a decrease. Falling numbers occurred until March, when a minimum was recorded. March also showed a decrease in numbers over February on the Riamugasire round. After this month, in April and May, as on the Riamugasire round, the numbers of the Bweli round rose, but then instead of a general decrease, numbers went on rising until August, when the round was last done " (Lloyd).

(b) A riverine locality on the Kuja river and its tributaries in South Kavirondo.

G. palpalis (called by the Jaluo " maügo ") occurs in high density in, and bordering on, the dense wooding of the Kuja river and in fair density on its more lightly wooded tributaries. Sleeping sickness still occurs in this area.

The streams are bordered in varying, but sometimes very great, width by close thickets of *Rhus glaucescens*, *Carissa edulis*, *Aberia* sp., and *Teclea nobilis*; these are the dominant species; also some *Clausena anisata*, *Allophyllus*, *Euclea*, *Phyllanthus*, *Grewia*, *Pavetta*, and other genera, bound sometimes with climbing *Jasminum* or *Rhoicissus*. There is often little overhead tree shade. The region, which the streams with their thicket traverse, is grass country grazed by the cattle of the Jaluo. It is mostly very open with scattered large trees, such as figs, *Kigelia*, and *Erythrina tomentosa*. In parts there is definite wooding—very open or less so—of *Acacia hebecladoides* (often dominat-

ing) or *Albizzia sassa*, *Bauhinia Thonningii*, *Anona senegalensis*, *Acacia stenocarpa*, much *Combretum Zeyheri*, and some *C. splendens*. In places, *Acacia Seyal*, *A. usambarensis*, and *A. campylacantha*.

The lower ground, with its combination of *A. hebecladoides* with *Rhus–Carissa* thicket, is reminiscent of the *morsitans* country of Ankole, except that the thicket is more concentrated on the streams and that *G. palpalis* occupies the thicket while *G. morsitans* uses the savanna.

The food animals and feeding-grounds include reedbuck, bushbuck, bush-pig, duiker, much waterbuck, many monitor lizards, and, at least on the Kuja, crocodiles, which frequent or visit the streams. Natives and their cattle visit or cross them also.

The flies scour the stream-banks for food and use small clearings as feeding-grounds also. The incidence of old females, pregnant and otherwise, at man is far greater than on Riamugasire. Thus, crossing the Odielo drift on 18th May, 1932, my fly boys caught 17 females to 4 males, the latter averaging approximately to the high hunger-stage iv.* The flies were obviously habituated to the constant passage of natives and had adopted the place as a feeding-ground.

The flies rest and breed in the thickets. The river and river tributaries in the locality visited (that is the Ndthiwa, Pala, Mwirogi, Odielo, and Wanjawa streams and the Kuja river) offer great variation in width of bordering thicket, and pupae have been found distributed as widely.

Times of activity are apparently different on the Kuja from those of Riamugasire. The flies become active later in the morning, apparently because of lower temperatures, and remain active through the hot hours at least up to noon.

7.—DRY-SEASON CONTRACTION BY *G. PALPALIS*.

Seasonal contraction definitely does take place where massive wooding is absent or food-supply emigrates completely; and such contraction is associated with dry-season conditions.

Amongst the localities in which this happens are Katwe in Uganda, and the upper reaches of the tributaries of the Kuja in Kenya. " Along the Sudan–Uganda border . . . there is a very definite wet and dry season succession and shrinkage of the distribution " (G. D. H. Carpenter *in litt.*). The following gives an idea of the types evacuated on the Kuja.

" Block 1 " on the Ndthiwa tributary below the Kaniandoto Dispensary is divisible into three :—

(*a*) There is a wide expanse of herbaceous and semi-herbaceous growth—half-shrub *Dombeya* and *Vernonia*, *Aspilia*, *Asparagus*, *Bidens*, *Hibiscus*, a fleshy *Acalypha*, *Ipomoea*, and castor-oil plant (*Ricinus*), grass-lined outside with scattered, small, dainty *Acacia stenocarpa* and with an odd *A. campylocantha* near the stream;

(*b*) in low scrub re-growth after clearing, further down, are *Rhus glaucescens*, *Carissa edulis*, *Clausena anisata*, *Bridelia*, *Maesa lanceolata*, *Aeschynomene*, *Gymnosporia*, *Allophyllus*, *Phyllanthus* and *Euclea*, and much *Acacia Seyal* further back; the stream so far is narrow, deep-cut, and much overhung by the scrub, half its length having been pools; the spoor of a bushbuck and a bush-pig have been seen in its bed;

(*c*) semi-herbaceous vegetation again—*Acalypha*, *Leonotis* and *Aspilia* scrub—river no longer tunnelled, broader water, a hippopotamus formerly—breaks—open fords—scrub, broken up—grass and the shrub *Hoslundia*—cattle.

* See p. 38.

Walking down through these types on 1st December, 1933, on a dull morning, whirling hygrometer readings varying from 76 and 70 to 77 and 69, Jackson and I took 15 flies in the herbaceous section, section (*a*) above (young % 29·4, female % of old flies 33·3, hunger average of old males only 3·25, but the whole with a feeding-ground aspect). In the first scrub section, section (*b*) above, 4 flies were taken—1 old female, 2 old males, and 1 young male. In the more open section with breaks and fords, section (*c*) above, 4 flies were taken—3 females and 1 young male—a more typical feeding-ground catch. Ten of the total of 26 were recaptures, previously marked locally and evidently at the time fairly resident. But " during the dry season at present the flies come down from the upper reaches and take refuge in the heavier bush lower down " (R. T. Vane *in litt.*, 7.ii.34).

Then comes a clearing and Block 2. The heavier bush, in Block 2, consists of fully matured thicket with undergrowth of rain-forest aspect but largely of the species listed for the scrub section, section (*b*) above, some over-shade (*Albizzia sassa* and other trees), stream again deep-cut, well shaded. Fly infestation here permanent; great width of thicket, flies little seen in its outside zone, next the savanna, but pupae much more numerous there.

The dry-weather contraction of *G. palpalis* is nowhere (to my knowledge) comparable with that of *G. morsitans*, but it is nevertheless very marked in northern Uganda (Carpenter). Vane also has informed me that along the Kuja " in the dry season the fly confines itself mainly to the heavy thickets and the river beds. During the wet season, the fly drifts from the true habitats and encroaches on the light thickets and bush skirting the edges. . . . During the rains the fly tends to migrate further up-stream."

8.—THE EFFECT OF VARYING LAKE-LEVEL.

From July 1933 to May 1934 Lloyd noted that the lake-level on Riamugasire had gone down about a foot. It was interesting that large portions of land formerly under water, now dry, had already become covered with a thick growth of herbs and shrubs. The maximum distance that the lake had receded was about five yards. No beaches of the Uganda type were exposed.

Chorley wrote in September 1932 from Uganda as follows :—

" This year's high lake appears to have resulted in a gradual decrease of the flies throughout the infested areas. The water has covered many of the sand and gravel beaches that formed permanent breeding-grounds. On the other hand, many of the old beaches on islands and mainland that lay back from the lake have come into increased use. Where these are absent the females are compelled to seek new places, many of them perhaps not very suitable. Annual variations in lake-level average about one foot. The difference between ' high lake ' and ' low ' may be as much as four feet. During low level large sandy beaches are exposed round the islands, the growth of vegetation on them is rapid, and the flies increase enormously. I am of opinion that during high lake-level the more scattered flies will be harder to control and reduce than by trapping at other times. It would be interesting to record the difference in the density of the flies that the construction of the proposed Albert Dam on the Nile will bring about." Carpenter gives the seasonal variation as from 1 to 3 feet.

9.—GRASS FIRES AND GRASS-FIRE PREVENTION IN RELATION TO *G. PALPALIS*.

Towards the end of September 1934 a fire broke out on Riamugasire Island. It was confined mainly to the northernmost hill (a breeding-ground)

and scarcely touched the general fly haunts, but it was of interest as showing what would have happened if it had done so. It was a ground fire, and the chief fuel was the rich older humus and the dead vegetable debris on top of it. It burned for over a week and defied Lloyd's daily efforts to extinguish it, neither did it succumb to a shower of 0·15 inches of rain. Water and trenching were the only means found of use. Time and again it was thought that it was out, but it was smouldering far under the surface, and would break out again some distance further along like a heath-fire.

The humus was reduced to ashes that were from six inches to a foot in depth, great heat being given out in the process. Much of the soil on Riamugasire consists of nearly pure leaf-mould intermixed with rootlets and a few sand grains. This may go down to a depth of many inches or may be a covering of only an inch over pure sand. All the main breeding-sites of *G. palpalis* on Riamugasire are in this rich humus. Fire going through such places would destroy every pupa, but would have little effect on the fly on the wing. Lloyd suggested the general burning off of the humus for the destruction of the fly's breeding-places and the production of an ash layer which, he thinks likely from observation, would be deterrent to larviposition. Whatever the effect of this on Riamugasire it would probably, even there, be but temporary and the asset of the humus would be lost.

Generally speaking, manipulation of the grass fires, whether by prevention or intensification, has little application for this fly, seeing that such fires are already excluded from, and incapable of burning, the great bulk of its haunts. Part 8, Section B, on pp. 440–443 below, should be consulted for a description of the experiments actually in hand for the destruction of *G. palpalis*.

10.—THE MATING ORGANISATION OF *G. PALPALIS*.

The mating organisation of *G. palpalis* may be deduced from what has been said already of the habits of this species. While the hungry flies of both sexes hunt vigorously the margins of the water and of open spaces in wooding for food animals, the unhungry "loitering" males haunt these hunting routes, wherever the shade is sufficient for comfort, to intercept feeding females. In addition they form "following swarms" about individuals of the favoured species of food animals—such as crocodile, *Varanus* lizard, tortoise, and situtunga—also for the purpose of intercepting females coming to feed. These mating assemblages form not merely at animals on land but also at crocodiles basking on rocks or lying in water with only their heads out. H. Lloyd has never seen them form on hippopotamus in water; these, as a rule, kept their heads out of the water for lesser periods than crocodiles.

11.—THE DISPERSAL OF *G. PALPALIS*.

There is abundant provision for dispersal in the food-searching movements of the flies. These take place along good margins and bad, for apparently indefinite distances, and it is probable that Fiske's simile of the desert spring, already referred to, is a true one. "Anything . . . which is conducive to increased rate of reproduction leads to increased density of infestation at and near the source of it and to wider dispersion." The flies that disperse may join or found new foci or may perish. It is probable that, as with the other tsetses, lack of food animals producing hunger is a most powerful incentive to dispersal. Lloyd found that the hungriest flies were those he took furthest from the shore over the surface of the lake. Carriage on animals and on canoes is doubtless of some small importance.

Lloyd carried out an experiment on Riamugasire which threw light on the rate of dispersal—not of hungry flies necessarily but of average individuals —over land. During his trial of screens, 4,362 flies, from screens and from the control, were captured and released with a differential mark for each day. Up to about 10 days after marking, the flies were found in greater numbers on the two sections of the fly round that overlapped the experiment; but after 10 days marked flies were no commoner on these two sections than elsewhere, indicating that on Riamugasire Island dispersal is complete after ten days.

The clearing—very complete—between Blocks 1 and 2 on the Ndthiwa stream was being crossed by the flies. They may have followed the stream bed, which contains alternately black boulders and pools and is therefore very conspicuous. Further, the tall herbaceous growth that had clothed the river-side before slashing regenerates rapidly, and would attract and guide the tsetses. Flies crossed also (Symes and Vane) open savanna wooding between the Pala and Ndthiwa streams, and their readiness to traverse grass country on dull days has been testified to by Chorley. Flies will cross a 300-yard channel of water.

12.—SUMMARY AS REGARDS *G. PALPALIS.*

We have in *G. palpalis* a notable carrier of sleeping sickness that is mostly found on the shores of rivers and lakes but may occur quite far back from them. It requires a combination of several types of country, one of which must be relatively massive wooding or thicket, of more or less evergreen type; it searches over water margins as well as on land and lives mainly on reptiles, but can live on mammals as well. Man is not one of its favoured hosts, but it will feed on him freely if sufficiently hungry at points where he can regularly be found; in our observations on Riamugasire and in Carpenter's observations in Uganda, this species is most active and hungry during periods of high temperature and not very high saturation deficit, yet was reduced greatly in density during periods of high saturation deficit though both hunger and female percentage in flies coming to man were low. It cannot be attacked at all generally by fire or by the prevention of fire, but it comes readily to traps and, being linear in its usual distribution, can perhaps in some places be attacked also by the severance from each other of its several vegetational needs, or by the thinning of the heavier shade on which it depends, where this is limited in extent. It has been successfully attacked by means of screens and hand-catching.

13.—THE ECONOMIC IMPORTANCE OF *G. PALPALIS* AS DEDUCED FROM OBSERVATIONS IN TANGANYIKA AND FROM ITS DISTRIBUTION.

G. palpalis is of little importance in relation to cattle, which are capable of living in its presence; but its importance as a carrier of *gambiense* sleeping sickness was abundantly proved in the outbreak round Lake Victoria in the very early years of this century. In that epidemic over 200,000 out of 300,000 inhabitants of the islands and mainland of Uganda are said to have perished, and the evacuation of the population from this region by the Government in Uganda, and on its own initiative from the infected areas in Kenya, " resulted in the loss to agriculture of the wonderfully fertile land along rivers and shores " (C. B. Symes).

In its distribution, *G. palpalis* covers an enormous area in Africa, but it occurs chiefly in the Congo and in west Africa. In east Africa it infests the shores of the Nile and the secondary Uganda lakes, as well as those of Lake

Victoria, Lake Tanganyika, and Lake Rudolph. It occurs also in the Anglo-Egyptian Sudan (Mongalla District) and in north-east Northern Rhodesia (right bank of Luapula river, running into Lake Mweru). It is important here chiefly through the fact that Lake Victoria in particular is the hub of large populations and will probably in the future nurse on its shores, which are fertile and accessible to transport, populations of a size yet undreamed of, the progeny of the Jaluo, the Baganda and the Wasukuma. By that time these populations will have automatically killed out a fly that merely needs foreshore clearing to exterminate it. In the meantime sleeping sickness is a danger, and such measures as are now being attempted on the Kuja river (*see* pp. 443–445 below) and Maboko Island have for their object the elimination of the flies by cheap methods in preparation for the admission of population and for application as well to the far greater and more difficult riverine areas of central and west Africa. So far as the Congo is concerned it is inconceivable that it also, with its fertile soil and waterways, should not, if civilisation keeps its grip on the country for (say) 300 years more, be the cradle of a vast population that will finally kill out this tsetse.

J.—THE RELATION OF *GLOSSINA BREVIPALPIS* NEWSTEAD TO ITS INANIMATE ENVIRONMENT.

1.—THE VEGETATIONAL TYPES WHICH *G. BREVIPALPIS* CANNOT INHABIT.

G. brevipalpis has not been seen in any savannas in which thickets are scarce or very generally light in character. It may be the general absence of heavy thicket which produces the absence of this tsetse from the greater part of the huge miombo-*morsitans* area of western Tanganyika Territory, so far as observations yet go.

Except on the rivers Rowana, Mbarangeti, Suguti, and Charano, flowing into Lake Victoria, *G. brevipalpis* has not been found in thorn-bush with *G. swynnertoni*, despite the presence often of quite heavy riverine thicket. It is probable that the desiccation here is too intensive during part of the year. It occurs in thorn-bush elsewhere with *G. pallidipes*, under conditions perhaps more moist locally.

2.—THE VEGETATIONAL HABITAT OF *G. BREVIPALPIS*.

Little intensive work has been done on this fly since I studied it in North Mossurise (Swynnerton, 1921), except by Wallace below Amani in 1926, though it has been met with by us in various localities; some work was done on it in Kilosa (D. W. Bishopp and Swynnerton) and at Musoma (Jackson and Lloyd), and it has figured in small numbers in the work on Maboko Island. It is dependent on the presence of heavy thicket, with or without overhead tree-canopy, and on lighter thicket types with this canopy. Its coverts may either be extensive, the flies utilising their margins for considerable distances in, or be mere scattered clumps, though usually in this case they are heavy, of evergreen or semi-evergreen type. *G. brevipalpis* differs from *G. pallidipes* and (less so) from *G. austeni* in the heavier calibre of the cover that it seems (on the whole) to require. Thickets on eluvium and alluvium are alike utilised.

Some of the situations in which I have found this fly have been the edges, and breaks in the edges, of rain forest; for some distance into dense-forest types not possessing the weight of full rain forest; in riverine (" gallery ") forest and riverine thicket of various kinds; in scattered evergreen or semi-evergreen thicket—often with woody lianas under the coils of which the flies

rest *—occurring in any sort of wooding; in the rains (in Kilosa) in deciduous thicket in miombo that in the dry season is raked by the fires; in dense, over-shaded patches of tree saplings in good wooding of *Isoberlinia–Brachystegia*, which latter may be infested throughout when these and other thickets are frequent (parts of Mossurise in Portuguese East Africa and between Dar-es-Salaam and Utete); in thicket coverts of varying heights and densities on or lying back from the shores of Lake Victoria, whether on islands or mainland streams; in the "coastal debris" (*see* map 1) of the old Arab plantations that were ruined by the liberation of the slaves and in which to-day mangoes, cashew-nut trees and coconut palms are mingled with a varied admixture of regenerating indigenous types belonging both to savanna and dense thicket.

The presence of water anywhere near does not appear to be a necessity, but coverts acceptable to the species frequently grow beside water. "I have found it waiting in all the [suitable] thickets at some distance from water of any kind and in hot weather in September with the ground baked. It is not at all dependent on the presence of vlei. Clean-stemmed wooding, however dark, was avoided in the absence of thickets" (Swynnerton, 1921).

In Zululand "*G. brevipalpis* is found in those parts of the country where the rivers and lakes are fringed with a heavier type of bush which, intermingling with large trees, supplies denser shade conditions than are found in the low bush savanna country" (Harris, 1930*a* : 13).

3.—THE USE MADE BY *G. BREVIPALPIS* OF THE SEVERAL PLANT COMMUNITIES WHICH MAKE UP ITS VEGETATIONAL HABITAT.

(a) General.

The description of a "mountain habitat" † given for *G. austeni* on p. 114 above applies also to *G. brevipalpis*, which was taken there in even greater numbers. The following reduction by Wallace of his figures for that area to a 12-hour period gives an indication of the relative use made of four types of country by these two flies. They are given in order of preference for *G. brevipalpis*.

TABLE 27.

Wallace's captures of *G. brevipalpis* and *G. austeni* reduced to 12-hour periods.

Type of vegetation	*G. brevipalpis*				*G. austeni*			
	♂	♀	Total	♀ %	♂	♀	Total	♀ %
Edge of *Manihot glaziovii* plantation . . .	168	36	204	12	40	37	77	48
Tectona grandis plantation with rocks . . .	126	48	174	28	12	16	28	57
Edge of mixed thicket .	126	12	138	9	27	33	60	55
Abandoned cultivation, partly burned . .	41	16	57	28	23	46	69	67

"The relatively largest numbers of *G. brevipalpis* were collected inside the edge of the *Manihot glaziovii* plantation. But . . . when this plantation was penetrated further fewer flies were caught. The *Tectona grandis* plantation yielded a slightly smaller catch. The neighbouring vegetation and the presence of possible breeding-places have influenced the number here, for in another

* See fig. 16. † This is shown in pl. 6.

T. grandis plantation, on the other bank of the river Zigi, practically no flies were caught on two visits." The latter place differed in being brighter below and in having no likely breeding-places.

" Fewer *G. brevipalpis* were taken in the edge of the secondary thicket. In the abandoned shamba area, a much smaller number of *G. brevipalpis* were collected, and, judging by observations made in other parts of this area, the important factor was the proximity of plantation or forest. In all other types of vegetation [*see* table on p. 164], only small numbers of *G. brevipalpis* were collected; here also, the proximity of forest growth decided the numbers of the flies to a great extent. In savanna wooding, separated from forest by shambas under cultivation or abandoned, a negligible number were collected " (Wallace, 1926).

Areas covered by low-growing crops, low bushes or grass, but with trees absent from the neighbourhood, equally fully searched, failed to yield either *G. brevipalpis* or *G. austeni.* The margins of rain forest could harbour *G. brevipalpis* at least, other factors, such as hosts for the fly, being suitable.

The total capture of *G. brevipalpis* made by Wallace was 947, of which 726 were males and 221 (or 23·4%) females, as against the figures for *G. austeni* of 421, 184, 237 and 56·2% (or more than double the female percentage). The figures were obtained in exactly the same period, exactly the same places, by the same methods and catches, and with the same bait-cattle. The same relative reluctance to use unbroken rain forest (20 miles traversed), in the late rainy season at least, was shown as in the case of *G. austeni.* Strong differences in the relative use of the different bush types may be seen in the tables given.

(b) The rest-haunt.

I failed to find puparia in a large proportion of the smaller, less-furnished rest-haunts (as the *Isoberlinia–Brachystegia* sapling thickets) in which I located this fly. It is therefore possible that a broad line can be drawn between rest-haunt that will be used for breeding—or at least can be safely so used—and rest-haunt that will not—or cannot be so used.

(c) The breeding-grounds.

Most of the types of thicket which have been enumerated already under the " vegetational habitat of *G. brevipalpis* " are used by this species as rest-haunts, whether for epigamic loitering, concealment, or breeding. " The species rests in the daytime scattered through all the little thickets in the bush it frequents, two or three or more to each." It was found " in greater numbers near certain little streams than in the *Brachystegia* thickets " [that is, thickets, sapling or otherwise, dotted through the general *Brachystegia*], " but (as similar results from the same type of forest away from streams appeared to show conclusively) this was only because these streams were lined with fringing forest of primary type " (Swynnerton 1921 : 355 and 344).

(d) The furniture of the rest-haunt and breeding-grounds.

I have found the flies resting under liana coils and in holes and bark-grooves of trees. The pupae have been found anywhere in the humus of dense thicket with much low cover, but especially under the extra-low shelter afforded by coils of lianas near the ground, the base of thicket stems, the forked roots of large trees, trunks overleaning the ground, and fallen trees—always, however, under good overhead shade.

At Nyabangi, on the shore of Mara Bay west of Musoma, there is a very small strip of varyingly dense vegetation which at all times contains *G. brevipalpis.* Breeding takes place here even under a ground litter of leaves in the shade of some low-foliaged mango trees without undergrowth. Rock shelters at the base of a granite kopje close by yield pupae also. Despite the case of the mango trees, the relative mortality under which is unknown, it is doubtful if adequate shade without adequate furniture would, over any great area, be favourable to survival—or if, at least, it would be at all freely utilised. How much furniture, or in how widely spaced patches, will suffice per mile of loitering-ground margin or square mile of savanna wooding is unknown.

On Maboko Island the *brevipalpis* pupae found in my searches for the pupae of *G. palpalis* between the 17th and 19th of January, 1933, were as follows :—

TABLE 28.

Numbers of pupae of *G. brevipalpis* found under different conditions.

	Sq. yards searched	Total *G. brevipalpis*	Puparia per sq. yard	Full *G. brevipalpis* pupae
(*a*) Dry thicket on upper hill-side .	100	21	0·2	0
(*b*) Dry thicket on hill-top . .	150	70	0·5	0
(*c*) *G. palpalis* rest-haunt by lake-side (damp thicket) . .	200	24	0·1	6
(*d*) *G. palpalis* rest-haunt by lake-side (damp thicket) . .	100	3	0·03	1

It will be noted that the largest number of pupal shells was taken towards the hill-top, but that, as with *G. palpalis* also, present breeding was by the lake shore.

(e) The feeding-grounds.

The tree savannas outside their thickets appear to be the hunting-grounds of the flies in their active hours. " Just at sunset the males emerge from the thickets in the neighbourhood of game and other paths and (where plentiful) distribute themselves at short intervals along them, sometimes for a considerable distance. As one walks each male moves on in front of one for at most a few feet, evidently scanning the walker for any females that may be with him, then falls behind " (Swynnerton, 1921 : 356). The queues of loitering males cease to be seen when one enters generally open conditions. Unlike what happens with *G. morsitans*, the " following swarm " does not follow man but, with cattle present, individuals from a queue may follow for great distances—5¼ miles in one instance. They tend to leave when the proximity of thicket is re-entered. Hungry flies feed quickly and leave; but 820 yards was the longest distance traversed in an experiment in which these were released at bait-cattle.

(f) Evidence from the composition of a population of *G. brevipalpis* near Amani as to the use to which different types of cover are put.

The available evidence as to the use to which different types of cover are put by *G. brevipalpis*, as deduced from the composition of a population near Amani, is summarised in the following table :—

TABLE 29.

Evidence from composition of a population of *G. brevipalpis* near Amani, as to the use to which different types of cover are put.

Locality	*G. brevipalpis* ♂	♀	Total	♀ %	Locality	*G. brevipalpis* ♂	♀	Total	♀ %
Rain forest	1	0	1	–	Regenerating rain forest	4	0	4	—
Cultivation, maize	5	0	5	—	Cultivation, cassava	5	2	7	29
Native cultivation, abandoned and burned through	56	27	83	33	Secondary dense forest types	153	44	197	22
Savanna wooding	1	3	4	75	Edge of plantation of Ceara rubber (*Manihot glaziovii*) most flies taken beside the more open, better-lighted conditions	212	45	257	18
Cananga odorata (Ilang-ilang scent)	43	12	55	22	Bamboos	2	4	6	67
Citrus spp.	1	0	1	—	Coconuts	6	0	6	—
Teak (*Tectona grandis*)	210	78	288	27	Banana shamba	4	1	5	20
Toon (*Cedrela odorata*)	20	5	25	20					

In the extract from Wallace's tables just given, the generally high male figures, compared with those for *G. austeni*, suggest strongly that (as was inevitable) Wallace met with the male-swarm complication afforded by the epigamic "queues," small and large, that one so often finds lined up along paths and in open spots from sunset onwards, awaiting, as is evident from what happens, the arrival of females that may join them or pass on animals.

If, nevertheless, we take female percentages above 25 as perhaps meaning some hunger we find that the open cassava (29%—total small), abandoned and burned-through cultivation (33% in the rather large total of 83 flies), savanna wooding (75% in a very diminutive total), teak, open below (27% in the large total of 288), and bamboos (clumps in open grass by teak —67% from (again) a diminutive total), suggest feeding-ground figures, though the teak (backed by forest and little above the suggested 25%) had breeding furniture of its own and foliage that hung fairly low.

In the secondary, mixed-thicket types and on the edge of the Ceara rubber plantation, both showing high totals (197 and 257), also the toon with undergrowth (total 25), and rain forest (totals 1 and 4 only, no females), the composition of the takings (♀♀ 22%, 18% and 20% for the mixed-thicket, rubber, and toon respectively) suggests rest-haunt conditions or a combination of loitering males with feeding-grounds. In the Ceara rubber it is interesting to note that at a depth further in than the marginal strip flies ceased to be taken at all freely. The Cananga (total 55, ♀ % only 22) was definitely an open plantation, but was traversed by a road such as would attract male queues from the rain-forest strip just behind.

The coconuts, citrus and maize (very open, totals in each case, small) gave male returns only—possibly male-swarm effect.

4.—TWO ISLAND LOCALITIES ON LAKE VICTORIA.

(a) Riamugasire Island.

G. brevipalpis was present on the occasion of my visit in 1922, but Lloyd, Jackson, and Moggridge found no flies of this species, or live pupae, in the two years (March 1933–November 1934) during which, between them, they worked on the island. Numerous old empty pupa-shells were found, and the conclusion reached was that this fly, which is still present on the Nyabangi coast nearly opposite, had become extinct in, or had abandoned, the island. No suggestion as to the cause is forthcoming.

(b) Maboko Island.

Going out with a net at dusk, one can capture a dozen examples of *G. brevipalpis*, showing that the density of this fly, which comes so little to man, must be fairly high. The numbers caught in our traps (evidently ineffective for this species) have been low but moderately steady. They are as follows :—1932, Oct.–Dec. : 2, 5, 5. 1933, Jan.–June : 7, 11, 5, 10, 2, 0; July–Dec. : 14, 12, 13, 10, 10, 13. 1934, Jan.–June : 26, 12, 12, 13, 16, 14; July–Oct. : 8, 14, 44, 68 (24 ♂, 44 ♀)—though none were taken on fly rounds in the last two months. There was no equivalent rise in those two months in the trap takings of *G. palpalis*.

It is not known to what extent the species utilises the reptiles of the island. It probably feeds on hippopotamus, for Milambo reports that on any nights on which these animals invade his garden, he takes numerous *G. brevipalpis* in his hut. Carpenter also (1924 : 191) records finding these flies " haunting the places where hippos sleep in the dense bush or awaiting their passage along the low tunnels which their frequent journeys keep open." They could be taken also sitting " head upwards on the trunks of trees in the open spaces under which the hippos sleep." He regards *G. brevipalpis* as differing from *G. palpalis* in possessing a preference for mammalian blood.

5.—THE PHYSICAL FACTORS.

(a) The geological and elevational habitats as indicators of the physical factors.

The most diverse geological formations underlie the country of *G. brevipalpis*, extending from coastal and riverine alluvial and laval clays to the crystalline rocks of the plateau.

The elevation varies in Tanganyika Territory from sea-level to 3,720 feet beside Lake Victoria and 4,500 feet or perhaps higher on Mount Kitumbeni near Arusha. The temperature range of the species is obviously great. The rainfall range is fairly wide also. On the whole it is high, though *G. brevipalpis*, within its several ranges, is capable of seizing on suitably moist eco-climates in a fairly dry general climate. It occurs thus near the Pare Mountains and between Voi and Makindu.

(b) One of the standard climates under which *G. brevipalpis* exists.

The table given on p. 121 under *G. austeni* relates to a locality in which *G. brevipalpis* also abounds and may be taken to represent the rainfall and temperature of one of its many general climates.

(c) The eco-climate of a rest-haunt of *G. brevipalpis*.

I am greatly indebted to Mr. R. E. Moreau, Secretary of the Amani Institute, for having permitted me to see the manuscript of his paper " Some Eco-climatic data for Closed Evergreen Forest in Tropical Africa," since published (1935, *J. linn. Soc.* (*Zool.*), **39** : 285–293).

Moreau maintained records of temperature and humidity for over twelve months in 1931 and 1932, and secured several sets of light-intensity readings also. He made his measurements in what he called the " intermediate forest " at Amani at 3,000 feet and in the neighbouring " lowland forest " at 1,150 feet. In the intermediate forest, extensively unbroken, only one example of *G. brevipalpis* was taken by Wallace in a 20-mile search. The lowland forest, less tall and dense, with a canopy more open and uneven, carried in 1926 some *G. brevipalpis* in its edges and breaks, and is probably, as a solid

community in the highly humid climate of the east Usambaras, just on the line which separates the haunts of this fly from conditions that it cannot use. As suggested under *G. austeni*, "lowland" is here a relative term, for real lowland types exist also.

Temperature and humidity were recorded with thermohygrographs in screens 4 feet above the ground. Controls were in an open coffee plantation outside and at the Amani main station. For the light measurements the holophane lumeter was used.

Moreau summarises his observations as follows:—"In temperature the eco-climate is more equable [than the standard climate], with almost the same minima, but maxima about 3° C. lower all the year round. The relative humidity is not strikingly different from the standard for the locality, which is exceptionally high. In shade, with all sunflecks avoided, the visible light averages about 0·1% of full sunlight." This last, at Amani, was regarded as equivalent to 21,000 foot candles of the holophane lumeter.

The following are some of the details:—

TABLE 30.

Light intensity in "lowland forest."

In lowland forest		Mean light intensity in foot candles	Standard deviation	Percentage variation	No. of readings
Date	Period covered by readings				
12.xi.31	11.25–12.05	25·94	10·77	41·6	47
14.xii.31	12.00–12.50	29·39	13·08	47·0	54

"A few readings were obtained of over 50 f.c.; but under certain particularly dense patches of canopy reading after reading was obtained of under 10 f.c." This figure probably begins to approximate to that of the "nook-climate" * in the holes and grooves of the resting-haunt that at any rate in thickets of less than rain-forest type are certainly used by the resting females.

Owing to the exceptional height of the standard relative humidity for Amani in exposed places, approximate saturation was shown both within and without the forest during about 50% of the total hours during 11 months —48·6% inside and actually 51·5% outside. "Any difference in humidity that might be significant locally lies in the wider range outside than inside the forest. Thus, 85% of the total hours are above 80% R.H. inside the forest against 76% of the total hours outside. Inside the forest practically none of the hours below 80% R.H. is below 70% R.H.; but outside about 300 fall below 60%."

For temperature, "the forest maxima are consistently lower by 3° to 4° C." than in the control outside, "except in the very wet and cloudy month of May, when the difference is hardly more than 2° C. . . . The beginning of the rise towards the day maximum is slightly later inside the forest than outside, but the maximum is reached much later, generally not until 16·00 hours or even after that. Correspondingly, the decline from the day maximum to the night minimum tends to be much slower inside the forest than outside. A typical effect is that recorded on 6.xi.32. The temperature remained above 20° C. for 11 hours inside as well as outside the forest; but the maximum reached

* Ecidio-climate.

in the former was only 23° C. against 27° in the latter. Integrated into degrees-hours above 20° this would give 77 outside compared with 33 inside."

The daily temperature range inside the Lowland Forest follows that in the Intermediate. At its maximum it is about 2° C. In the control site in the coffee, "outside the Intermediate Forest, it is consistently above 9° C. from November to February, but in the cool wet month of May it is as low as 3° C. Inside that forest the mean daily range only once exceeds 6° C., and for April, May and June it is under 3°—in May less than 2°. Throughout the year the daily range outside is always at least 1½ times as great as it is inside; and it is in some months practically double."

Moreau concludes :—

> "The potentially significant divergence from the standard climate is in the maxima and in daily range, not in the minima. With the Intermediate Forest the differences in the maxima are actually equal to that caused by a difference of quite 2000 ft. in altitude. During a part of the year the daily range in two different types of closed evergreen forest may differ by half as much as the daily range under the denser canopy differs from that in open air."

These valuable pioneer observations, made in relation to the forest birds, record the general conditions in the forest undergrowth rather than in the still darker, cooler and (perhaps not in rain forest) moister bark-grooves, rot-holes, and liana undersides near the ground in which sheltering tsetse flies rest. The employment of thermocouples and Buxton's paper hygrometers would be necessary to get results thence, but it is most useful also to know something of the general forest undergrowth climate. Actually, it strikes one that as regards shade, temperature, and moisture, even *G. brevipalpis* might at times at Zigi or Amani live very pleasantly indeed in a Stevenson screen in the open. Further, it appears, however, that, inside such a screen in the sun, conditions would not be cooler than they often actually are outside in dull weather or in the evening, when *G. brevipalpis* does move about in the open. The comparison really needed is that between the forest undergrowth and sun conditions outside, it being these, obviously, which keep the tsetse (and, perhaps, the forest birds) under cover.

The forests studied by Moreau represent types which, when in bulk and unbroken, *G. brevipalpis* will not inhabit—probably not on account of an excess of humidity, which, if anything, is lower (at Amani) in the forest than outside it, but as a result of their uniformity. But the Lower Forest at least represents a type which, when interspersed with breaks and passages, the species is capable of using; and it is in any case of great interest to obtain a diagnosis of conditions which very definitely exclude *G. morsitans* and *G. swynnertoni.*

(d) The round of the seasons.

The figures given under *G. austeni* on pp. 121 and 123 above show briefly the temperature and humidity changes in the course of a year. However, beyond the observations already given incidentally, with the evidence of seasonal contraction and that afforded by the hours and habits of activity of the flies, little has been noted of the actual effect on *G. brevipalpis* of the physical factors and seasons.

(e) The hours and habits of activity and site of attack as possible indicators of requirements.

The hours and habits of activity may certainly afford indirect evidence of an insect's tolerance or intolerance of dryness and heat. I have confirmed in the

Tanganyika Territory my earlier conclusion (1921) that females of *G. brevipalpis* will only attack cattle passing close up to their thicket in the warmer hours and that in the evening they will wander out through the more open woodlands. "*G. brevipalpis*, as I found, attacks in the shade of the bush at any hour, but does not fly appreciably outside its own thicket to do so except in the early morning, after sunset and on dull or rainy days. Having attacked, even in sunny weather, it completes its object of feeding or riding, unless its victim emerges into the open. In this event it usually leaves. In a special experiment that I carried out with the aid of a lantern occasionally lit and turned on I found that both this fly and *G. pallidipes* attacked right up to dark. Then every fly suddenly disappeared. On moonlight nights they continued their attacks" and "the cattle sustained early morning attacks (before sunrise) from both *G. brevipalpis* and *G. pallidipes* with the thermometer at 47° F. and under" (Swynnerton, 1921 : 360).

Wallace records for Amani that "*G. brevipalpis* is more abundant in the evening and least abundant in the heat of the day." Observations by Jackson, by myself and by the fly boys, on various occasions on Maboko Island in the Kavirondo Gulf of Lake Victoria, have confirmed quite strongly also the belief that *G. brevipalpis* scours the savannas on warm moonlight nights: numbers of the flies on some moonlight nights came to the illuminated undersurface of our tents, though these were well above and out of sight of any thickets in which this tsetse was seen in the evenings.

It is probable that where they occur together there is an inverse relation between this fly and some of the other tsetses in their use of feeding-grounds, the latter using them, say, from 8 a.m. till dark, and *G. brevipalpis* using them from sunset till 8 a.m. The figures given in the tables under *G. austeni* (p. 122 above) from 8 a.m. to 7 p.m. may be taken broadly to apply to the chief hours of rest of *G. brevipalpis* and from 6 p.m. to 8 a.m. to its probable hours of activity on moonlight nights. H. Lloyd found this inverse relation to be very striking as between *G. brevipalpis* and *G. palpalis* on Maboko, the one fly each day disappearing as the other appeared.

The part of the body on which this tsetse attacks an animal may be a possible indication of its requirements; this is the median line of the belly or between the fore or hind pair of limbs, and is probably a matter of shade-requirement rather than thinness of skin, for a tsetse can feed on a rhinoceros.

(f) Season as a cause of concentration and shifting on the part of *G. brevipalpis*.

Of *G. brevipalpis*, as of *G. austeni*, Wallace noted a retraction when the heavy rains had given place to periodic showers. I myself (1921) noted the practical disappearance of this fly in the dry season from a considerable area, which was (i) deciduous and (ii) subject to a temperature that approached freezing; though it has been noted repeatedly also that, as an obvious activity effect due probably to hunger-thirst, *G. brevipalpis*, like *G. pallidipes*, appears to man in larger numbers in the late dry season than in the rains. Jackson correlates the appearance of *G. brevipalpis* to man with low humidity readings on Maboko Island and notes in a report (22.ii.34) that in Musoma "high catches have been made on dry days and no flies could be caught on wet ones, although flies were seen and heard flying round. Specimens have since been found by searching tree-trunks on damp days." It is probable that for *G. brevipalpis*, as for the other species, special dry-season cover is necessary.

In June and July *G. brevipalpis* was seen to avoid riverine wooding on

latitude 20. "I found no *brevipalpis* and only once a *pallidipes* in the immediate neighbourhood of river banks west of the Sitatongas; I refer to such [big] rivers as the Buzi, not mere overshaded streams like the Inyamarimu. Yet on getting a bit back from the river, fly (mainly *brevipalpis*) was found generally and in quantity and thence up the hills to the limit of the suitable bush. There seemed to be a definite avoidance of the big rivers—possibly a matter of the greater winter cold in their vicinity" (Swynnerton, 1921 : 350). At least no other factor could be thought of.

6.—GRASS FIRES AND GRASS-FIRE PREVENTION AS A MEANS OF CONTROLLING FLY COVER.

(a) Organised grass-burning as a means of setting back the succession.

There are certain areas (as in Mossurise) in which the scattered *brevipalpis* thickets are relatively small, and are flanked by such long grass that even the normal burnings probably reduce seasonally the range of *G. brevipalpis*, while a course of late burning linked with some clearing or with discriminative clearing alone, might so alter conditions in the thickets as to drive it out altogether. There are great areas, on the other hand, in which the thicket is probably in general too massive for either burning or clearing to set back the succession sufficiently generally to affect the insect adequately under the conditions in Tanganyika.

(b) The cessation of grass-burning as a means of advancing the succession.

If country were to become generally covered with dense thicket or closed forest through the prevention of grass-burning combined with the drainage of seasonal swamp, it would broadly depend on how unbroken was the result whether the latter would favour the extension of *G. brevipalpis* or would act as an exterminative measure. Our observations near Amani suggest that continuously solid close covert without any interspersion of examples of the earlier successional stages might have the latter effect even on this species of tsetse, although, without planting of the mbugas as well as their drainage, it might take a very long time. It would be necessary also to attempt to institute a strict control of the pigs that would continue to utilise the contacts of the forest with areas and patches of native cultivation, thus rendering these contacts useful to the tsetse as well, and also to prevent the upkeep, by game concentration, of fly feeding-grounds in the forest. The fact that not every type of thicket suits *G. brevipalpis*—or suits it all the year round—suggests the study first of the types of cover that could be locally produced by prevention of burning.

7.—THE MATING ORGANISATION OF *G. BREVIPALPIS*.

Our one indication regarding the mating organisation of this species is provided by the queues of male flies, with occasional females, which from sunset onwards form on paths leading through the general savanna in which the "rest" thickets are situated. A walker will find the individual flies moving on in front of him along the path for a little while but shortly dropping behind. There can be little doubt that this habit provides for the meeting of the sexes by means of a rendezvous. Animals passing along are apparently inspected for females that may be on them and virgin females appear also to join these queues.

8.—THE DISPERSAL OF *G. BREVIPALPIS*.

(a) Dispersal by independent movement.

Nothing definite has yet been learned about the independent movement of this species. There is no movement on sunny days. There certainly is movement on moonlight nights. If the species is as active on such nights as is suggested, there is no reason why, with the low temperatures and saturation deficits then existing, it should not cross or hunt over water and open spaces and incidentally extend its habitat.

(b) Dispersal by following.

" On the 16th May a *G. brevipalpis* followed the two bait-cattle for one mile. In doing so the fly moved from an area of *Manihot glaziovii* plantations into primary forest " (Wallace, 1926). " So dependent does the fly appear to be on good shade that, except in the early morning, after sunset and on dull days, it will leave animals it is on as soon as they emerge from the shady bush into the sunlight. On dull and rainy days it will follow freely into the most open country and at high noon, so that the term ' crepuscular,' which has been applied to this fly, is not altogether justified by my observations " (Swynnerton, 1921 : 344).

" Males of *brevipalpis* waiting on game paths (near thicket) were frequently tempted to attach themselves to the cattle and would then often ride for quite a distance. . . . I measured one of these rides by five male *brevipalpis* in dull weather, first marking each of them with a dab of white paint. The flies had come to us just before and were following, not feeding. The greatest distance travelled was 5¼ miles by the one fly that stayed to the end. All five flies were still present at 4 miles and 700 yards. Every kind of country was traversed, *brevipalpis* bush, simple coppice and open grass. The flies deserted us on our getting back into their native bush. Elsewhere where *brevipalpis* had followed us into the open in the daytime it waited before leaving us until it had reached suitable bush, and an individual that once followed far to a camp in the open stayed about four hours (in the evening) before disappearing. All this was interesting in relation to the explanation of outbreaks of nagana in which it appeared that the fly had crossed much open country to bush-patches in the grazing-grounds or near a kraal " (*ibid.* : 357).

" Hungry flies, including, so far as I saw, *all* females, came to feed, not follow, and the longest distance travelled in an experiment in which I released a considerable number of hungry marked *brevipalpis* and a few *pallidipes* behind the cattle was 820 paces quickly covered. The other flies had already dropped off replete before that, in spite of the kicking and running on the part of the cattle " (*ibid.* : 357–358). Hippopotami are probably accompanied on land at night (see Milambo's observations on p. 165).

9.—SUMMARY AS REGARDS *G. BREVIPALPIS*.

G. brevipalpis is a fly which, by full daylight, at any rate, is more closely confined to the interior of thicket than is either *G. austeni* or *G. pallidipes*. At sunset it emerges and it would seem that on light, warm nights it scours the tree savannas and perhaps even the open plains and marginal waters of the lake. The extent to which the more open country is indispensable to its finding of food, given game concentration in the forest, is however another matter and one yet to be proved. Of the possibilities of control one can only at present say :—

(*a*) that traps, so far, have been useless;

(*b*) that the destruction or thinning of the heavier types of thicket or the overshade of lighter thickets appears to offer promise and that it has been shown by experiment that all actual trees can be left, but that in partially cleared thicket it is hard to prevent rapid regeneration;

(*c*) that the isolation of patches of thick country containing *G. brevipalpis* has been thought of, but the fact that the fly follows animals and perhaps moves of its own initiative across any sort of country at night may invalidate this;

(*d*) that a densification of country climatically favourable to the species by not burning the grass might, if it were sufficiently uniform, be unfavourable even to this species, but that concentration of game within the forest and beside native cultivation would probably have to be prevented and open mbuga would have to be drained, or (for speedier densification) drained and planted.

10.—THE ECONOMIC IMPORTANCE OF *G. BREVIPALPIS* AS DEDUCED FROM OBSERVATIONS IN TANGANYIKA AND FROM ITS DISTRIBUTION.

G. brevipalpis carries the trypanosomes of animal disease, although there are cases in which cattle have remained alive in its neighbourhood. It has been shown in the laboratory to be capable of carrying *Trypanosoma rhodesiense* also, but as it attacks man far less readily than any of the east African tsetses except *G. austeni*, it is probably of little importance in the latter connection.

In Tanganyika the distribution of *G. brevipalpis* is based on dense wooding and thickets on the shores and islands of Lake Victoria and on some of the rivers that flow into the latter. It is found again on Lake Tanganyika and in Mwaya at the north end of Lake Nyasa. It is found outside Tanganyika Territory in Nyasaland and the Belgian Congo; in north-east Northern Rhodesia (near Hargreaves and on the Petauke–Nkusha road); in northern Nigeria (Sokoto Province); and in Angola. Like *G. austeni*, it mainly inhabits, however, the great eastern tsetse belt in Kenya, Tanganyika, and Portuguese East Africa, occurring also in northern Zululand, and is found extending back great distances from the coast. It is likely that it will be found in all suitable situations, whether in miombo, thorn-bush or the denser communities, in the whole of this belt (*see* map 1). It occurs about the foot of the Usambara and Pare Mountains, in the Rau Forest near Moshi and elsewhere below Kilimanjaro, and on Mount Kitumbeni north-west of Arusha.

It is the third of the east African species of tsetse which offer the great disadvantage that they inhabit the heavy types of wooding associated with the late stages of vegetational succession and so, where they occur or can enter, may vitiate our attack on *G. morsitans* and *G. swynnertoni* by means of not burning the grass. But if the resultant cover could be made so uniformly dense that no interspersion would occur of open patches and types such as may serve it as feeding-grounds, even *G. brevipalpis* might go.

K.—THE RELATION OF *GLOSSINA FUSCIPLEURIS* AUSTEN TO ITS INANIMATE ENVIRONMENT.

1.—INTRODUCTORY.

Practically all that we know of the habits of *G. fuscipleuris* is derived from a single closely recorded observation of Burtt's and some observations of Lewis's (1934). Burtt, visiting the Kivu volcanoes from Kew during leave,

came across *G. fuscipleuris* in the valley of the Rutchuru river, which rises on Mount Mikeno in the " Parc National Albert " Gorilla Reserve, in the month of May at an elevation of about 5,000 feet. " My boy and myself," he reported, " were attacked immediately on arriving at the river by this large dark tsetse of which three were caught. . . . Between 8.30 and 9.0 a.m. four more were captured. . . . One fly was seen attacking a goat. . . . The fly settled above the hoof, also on the stomach, aided by the animal's movements in avoiding all our attempts at capture and being unusually persistent. The goat was restless, kicking violently as the fly bit it. . . . The fly is slow, emitting in flight a low note resembling that of a large *Haematopota.* When settled they allowed one to bring the hand to four inches from them without taking alarm, and were extraordinarily easy to capture by hand. . . . The flies settled on the legs of my boy and myself, who were the only two members of the party wearing khaki puttees. . . . None settled on any other part of our clothing or upon the 25 porters who wore soiled blankets with much of their body exposed. One male and six females were captured, and no doubt if time had been available this tsetse would have proved to be common."

Lewis found this species in several localities during his survey of the Masai Reserve in Kenya.

2.—THE VEGETATIONAL HABITAT OF *G. FUSCIPLEURIS* AND THE USE MADE BY IT OF THE ELEMENTS WHICH COMPOSE IT.

" Most of the Rutchuru River is clothed with dense impenetrable elephant-grass (*Pennisetum purpureum*) up to 14 feet high, forming veritable grass-jungle with scattered secondary thickets of *Acanthus arboreus* (a pink-flowered spiny-leaved shrub growing to 12 feet in height, very typical also of Uganda), *Vernonia podocoma* and *Cassia didymobotrya.* These shrubs supported a tangle of creepers—Convolvulaceae, Cucurbitaceae and *Thunbergia alata.* The river itself is fringed by a dense tall forest of *Albizzia zygia*, *Phoenix reclinata*, *Dolichandrone pachycalyx* and *Ficus* spp. A quarter of a mile up the river a broader gallery forest characterised by big trees of *Albizzia zygia* with *Spathodea nilotica* and evergreen undergrowth spread itself out. The wooding generally resembled very strongly the base-habitat of *G. brevipalpis* " (Burtt).

The fly has been recorded from forest country in Uganda and was described by Gerard (1920, quoted by Newstead, 1924) as having been found in the upper Lukuga (Belgian Congo) by little streams bordered by luxuriant vegetation.

Lewis (1934) states that he collected many specimens in Kenya " in the thick vegetation on the Mara River, usually in the backwaters and short gullies opening into the river. The atmosphere was humid, and the well-worn paths of game (buffalo, rhinoceros and lion) indicated that these places were utilised by numbers of animals coming to the river to drink. In the dense vegetation along the Upper Enderrit, and at 5,300 feet, three specimens were caught. On the east bank of the Mara—still in thick bush—six individuals were caught on a game-path near the junction of the Naitorr Lera and the Mara. Near a salt-lick (4,900 feet) at Ol Doinyo Burgoi, there is permanent swamp with an abundance of palms of the genus *Phoenix.* While resting in the shade of a palm, at 2 p.m., a single *G. fuscipleuris* attacked me. . . . At Erok (5,900 feet) two males and a female darted out of the thick bush near the Osinandei stream to my fly-boys at 11.30 a.m. At the Lolgorien camp, situated near the Mara and not far from another salt-lick my personal boy caught a male. . . . As we passed through a strip of forest, at an altitude of 5,900 feet or more, on the

descent from the Siria Hills to Lolgorien I captured a female *fuscipleuris* on my car. At the ford which crosses the Mogor, I saw many flies of this species. . . . The tributaries of the Mara, especially that known as the Shiater, seem to be infested with *G. fuscipleuris.*"

In the initial attack on Burtt's party, the latter was in the road that traversed the dense growth on the river. One of the captures was "in grass savanna with scattered trees and bushes of *Lantana salvifolia* clothing rising ground of volcanic ash." The attack on the goat was "in open maize fields near a native village."

3.—INDICATIONS AS TO PHYSICAL FACTORS.

The elevations are all high—5,000 feet (Burtt) and from 4,900 to 5,900 feet (Lewis). The indications are of high humidity also. The hours of attack extended throughout the day—8–9 a.m. (Burtt), 11.30 a.m., 2 p.m., and 7 p.m. (Lewis)—but the weather is in no case stated.

4.—SUMMARY OF OBSERVATIONS.

G. fuscipleuris would appear to base itself on dense thicket, dense forest, and especially gallery (riverine) forest strips, but to come into open savanna wooding and quite open fields, as also to roads, game-paths, and drinking-places, in order to find its prey when it is hungry. It thus uses at least two types of country at the same time (counting roads or drinking-places as one) and doubtless lives largely at their contacts. This fly evidently visits the more open country and attacks there quite freely in broad daylight, in this differing from *G. brevipalpis*. *G. fuscipleuris* would seem also from these and Gerard's observations in the Congo to attack man much more readily than that species.

5.—THE ECONOMIC IMPORTANCE OF *G. FUSCIPLEURIS*.

"The Masai stated that *G. fuscipleuris* attacks cattle very readily and they maintained that it transmitted disease to their stock" (Lewis, *ibid.*). It is obvious also that man is relatively readily attacked, and that the species may therefore be capable of transmitting sleeping sickness. It is quite widely distributed, having been taken in half a dozen localities in Uganda, in south-western Kenya, near Natron in Tanganyika, in three localities in the southern Sudan and a dozen in the eastern part of the Belgian Congo.

L.—THE RELATION OF *GLOSSINA FUSCA* (WALKER) TO ITS INANIMATE ENVIRONMENT.

1.—INTRODUCTORY.

None of us, of the Tsetse Research Department, have yet met with this tsetse in nature. Occurrences of *G. brevipalpis* have been so often ascribed to it that caution must be used in accepting recorded localities. It occurs in Uganda in the neighbourhood of Lakes Edward and George. Its alleged occurrences in Tanganyika Territory I ascribe in nearly all cases to *G. brevipalpis*, but a fly sent me from the east side of Lake Tanganyika by Capt. F. Collingwood of the Tanganyika Administration, and unfortunately later mislaid, appeared to me to be of this species and, being particularly dark-winged, probably to belong to its variety *congolensis* Newstead and Evans, which occurs just across the Lake.

"This West African species of tsetse enters the region under discussion only on the western boundaries of Uganda. It is not uncommon in the

forests of Toro and the Semliki Valley, and is also reported from the Budongo forest, Unyoro. . . ." (Neave, 1912 : 309.)

2.—THE VEGETATIONAL HABITAT OF *G. FUSCA*.

Schwetz has done most work on this species, in the Belgian Congo. According to him (1919), as quoted by Newstead (1924), this fly occurs only, apparently, in rain forest or its equivalent. This must, he says, be at least 200 metres wide and is mainly found along streams; but the species may also abound in such forest away from water. It appears to man almost only along paths and roads and is crepuscular in its habits, being seen from sunset onwards.

Dr. Neave tells me that his observations indicated that *G. fusca* uses denser forest than does *G. brevipalpis*; I have myself recorded (1923 : 309) that " From a limited experience of this insect it would appear to be essentially a dense forest, rather than a riverine, species, and evidently delights in very deep shade."

" On the other hand," Newstead writes, " Fell (1912) in Ashanti states that this species favours scrub and small forest, occurring between the dense jungle and orchard grass [?] bush; whilst Kinghorn (1911), also in Ashanti, found it on the fringes of patches of bush, and Graham (1907) from the same place describes it as frequenting the main roads and bush paths."

3.—THE USE MADE BY *G. FUSCA* OF THE ELEMENTS WHICH MAKE UP ITS VEGETATIONAL HABITAT.

(a) The rest-haunt and breeding-places.

Closed wooding, with rain forest (Schwetz) or scrub (Fell), evidently form the main rest-haunt and breeding-ground of this species. Evidently, too, paths and woods are amongst the places it uses as feeding-grounds, coming out to these in the evening as does *G. brevipalpis*. It is probably partly nocturnal—like the latter (see below). Its occurrence on the fringe of the bush is highly suggestive that vegetational contacts are favourable to it, just as they are with other species.

(b) The furniture of the rest-haunt and of the breeding-places.

It is likely from Schwetz's descriptions of the sites in which pupae were found that here also *G. fusca* differs little from *G. brevipalpis*. The bases of large trees and, especially, the crevices below the earth binding the roots of a large fallen tree, and of the ground below fallen trees slightly raised, were the most productive sites, but a pupa was found also under the plain leaf carpet " *dans un endroit ordinaire*," shaded and with scattered " *plantes vivaces* " (Hegh). All these observations were made in closed forest.

4.—INDICATIONS AS TO PHYSICAL FACTORS.

G. fusca, according to Newstead, has been recorded up to 5,000 feet: Neave writes (1912), " Though occurring in many places with *Glossina palpalis*, the distribution of these two species is by no means coincident, since *G. fusca* seems to be able to exist at considerably greater elevations and in much cooler localities. In Uganda the limit for this species seems to be about 4,500 feet, as compared with rather under 4,000 feet for *G. palpalis* in the same region. It is of course also numerous at much lower elevations, *e.g.*, the forested portions of the Semliki Valley at under 2,500 feet. It seems to feed principally in the

early morning and late evening and shows a decided preference for animals, as compared with man." Neave also believes that with *G. brevipalpis* and *G. longipennis*, *G. fusca* is probably nocturnal. Kinghorn (1911) met with it in dull weather and records it as biting at night (Newstead, 1924 : 89–91).

5.—SEASONAL MOVEMENT.

Schwetz (1919) observed that *G. fusca* at the approach of the dry season, emigrated from a wet-season haunt with deciduous trees and no permanent shade to one with dense shade and permanent water.

6.—SUMMARY AND ECONOMIC STATUS.

A summary of the existing data on this species, together with a note on its economic status, will be found on p. 484 below.

M.—NOTE ON *GLOSSINA LONGIPENNIS* CORTI.

Nothing has yet been done by the Tsetse Research Department on this semi-desert species, frequenting the drier types of the nyika or thorn-bush. Neave (1912 : 308) refers to its entering railway carriages at night, and says of its vegetational and physical requirements that " it appears to be absent from the sea-coast, where the climate is probably too humid for it. It would seem to be entirely independent of water, and indeed rather to avoid it. I found it most striking, when travelling from station to station on the railway between Voi and Makindu, to find numbers of this species in the dry, semi-desert, thorn-bush country between the rivers, while on the river banks it was replaced by *G. brevipalpis*. Like the other large species of *Glossina*, it is chiefly on the wing and inclined to feed in the early morning and late evening." T. J. Anderson, on the other hand (1921), found this fly in the Southern Masai Reserve, Kenya Colony, to be unexpectedly abundant on moist swampy flats and on the bank of a river.

This species is known to occur in Somaliland; Kenya Colony (Kibwezi and Guasa Nyiro river; Narossura river; Tsavo river; between Voi and Tsavo river; Thika-thika river; Kamo and Kinya Weil. Boran Galla country, river Welmal); and northern Uganda (Mt. Zulia).

N.—MAN-MADE FLY BELTS.

1.—SAVANNA FLY BELTS GENERALLY.

There are few fly ranges in east Africa that are not to some extent artificial, for the present-day distribution of the vegetational covering is mostly the result of man's past activities and of his present annual fires. Without the latter, density would in most places be sufficient to exclude at least *G. morsitans* and *G. swynnertoni*.

2.—A FLY BELT RESULTING FROM INTERSPERSAL BY MAN OF VEGETATIVE TYPES.

On the Usambara slopes, already described in connection with Wallace's investigation, man's hand has displayed its presence in the splitting of the old unbroken rain forest, uninfested by tsetse, into blocks and small patches and its interspersal in chess-board style with patches of cultivation and (fol-

lowing this where it is abandoned) tree-savannas, secondary thicket and grassland. This is well shown in pl. 6. The old unbroken forest, when it covered the slopes of the hills and the lowlands described immediately below, was probably as unsuited to tsetse as its larger remnants still are. The mixture of types of to-day carries large numbers of *G. brevipalpis* and *G. austeni* and smaller numbers of *G. pallidipes*.

3.—A COMPLETELY ARTIFICIAL FLY BELT.

Stretching from Tanga on either side of the railway line westward to Nyusi along the foot of the eastern Usambaras is a country of low hills and undulations, which owes its present fly infestation to its planting by man and its present close occupation by him. Natural *Dombeya-Anona* savanna and in places *Acacia* are present, sometimes extensively, but for the most part the country is one great, continuous steppe of native cultivation, a patchwork of small maize and cassava fields and small fallows. Such country under the climatic conditions of Shinyanga is bare and inhospitable to tsetse. Under the better rainfall of Muheza it is just the reverse. Bush at once springs up on the fallows, and the Mvule trees (*Chlorophora*), which are one of its early constituents, are allowed still to dot the landscape when cultivation is resumed; small clumps of citrus, mango, banana, and coconut palm are everywhere grown, while the cassava itself when tall affords shade and bare ground below. All dongas and banks tend to carry dense thicket, mostly low, while the sisal plantations between weedings grow a general beard of low shrubs, especially *Phyllanthus*. Above all the old German Ceara rubber plantations, untended and filled with undergrowth of their own seedlings and native shrubs, are so large and, in places, so numerous as to form one of the chief plant communities. With them may be classed later-formed plantations of *Cassia siamea* with similar undergrowth.

Animals, except goats, are extremely scarce. In a few spots cattle are kept, but they are mostly introductions for slaughter; more generally, they cannot be kept. Bush-pigs are the main and almost the only wild ungulate, holding their own in small to moderate numbers despite past wholesale attempts at netting them and continual present attack. Generally, this area is infested with *G. pallidipes* in small numbers, and more patchily with *G. brevipalpis* and *G. austeni*—the three species together seeming responsible for the absence of cattle. The flies are based largely on the rubber and other plantations, often in very great numbers, and *G. pallidipes*, at least, would seem to range the great areas of native cultivation with their landmarks of scattered trees and their secondary bases for the tsetse in the form of their orchards and taller cassava and the shrubs of their dongas. Moggridge's more extreme instance of the activities of this fly in areas of wide cultivation has been referred to on p. 104 above; and Muheza reminds one further of Johnson & Llewellyn Lloyd's conclusion on *G. tachinoides* (1923) that: " it . . . can thrive in densely populated districts where the wild fauna is reduced to as small proportions as it conceivably could be in tropical Africa."

To say that when intensive development comes in, the fly goes out, is therefore not always true. Whether the fly goes out depends on the nature of the development, and in this case, particularly, on the effect of the climate on the vegetation that can be grown and the regeneration of the natural vegetation. It probably also depends on the species of fly, for *G. morsitans* appears much more sensitive to the influence exerted by the presence of human settlement than do some of the other species.

O.—THE RELATIONS OF SOME OF THE TSETSES TO THE PHYSICAL FACTORS AS TESTED IN THE LABORATORY, AND SOME FIELD EXPERIMENTS.

1.—INTRODUCTORY.

In addition to the work on *G. morsitans* carried out at Kikore in 1930–32, described in his paper of 1933, Potts carried out a series of experiments in Shinyanga in 1934, the results of which are referred to below. The investigation was intended purely as a preliminary exploration of the effect of different temperatures and relative humidities on four species of tsetse (adults and pupae) under controlled conditions.

Some of Nash's observations on *G. morsitans* are also included below and, for comparison and greater completeness, quotations are made from Buxton & Lewis's recent fine paper (1934) on their experiments on *G. submorsitans* and *G. tachinoides* in Northern Nigeria.* Jackson has latterly carried laboratory methods into the field with some brilliance, but his results, which will take us a considerable step in our knowledge, are not, for the most part, available in time for inclusion here.

2.—THE SPECIES TESTED BY THE TSETSE RESEARCH DEPARTMENT, TANGANYIKA TERRITORY.

In Potts's work at Kikore in 1931–32 (published 1933) only *G. morsitans* was used. In 1934 in Shinyanga the observations were made on four species, the pupae of two of which were obtained in some numbers. These were *G. swynnertoni*, *G. morsitans*, *G. pallidipes* and *G. austeni*. Of the last, sixty pupae only were available.

3.—THE METHODS EMPLOYED IN 1934.

The effect of temperature on the flies and their pupae was investigated by Potts in two different ways :—

(*a*) by exposing them to a varying temperature which was measured continuously by means of a thermograph, under three different conditions :—(i) those of the laboratory, giving a diurnal range of temperature about the daily mean temperature of approximately 17° F. ; (ii) those of a screen in the instrument station, giving a diurnal range of 22° F., and (iii) those of the incubator room, giving a range of 2–3° F. only. The daily means of these three sets of conditions were very similar, the experiments showing therefore the effect of differences in diurnal range about the same daily mean.

(*b*) by exposure to a constant temperature by means (i) of the Incubator Room, during October and November; which then showed a mean daily range of only 0·6° F., the absolute maxima and minima recorded during the month of October being 79·6° F. and 78° F. respectively; (ii) of an incubator, giving temperatures of 82·4° F. and 87·8° F. ; and (iii) of a Wasserman bath, giving temperatures of 104° F. and 113° F.

Humidity was controlled by means of solutions of caustic potash. Humidity

* Whatever one's view may be as to the relationship of *G. submorsitans* to *G. morsitans*, it seems best in this section to treat them as distinct, because Buxton and Lewis from whom I quote, have done so. Nash's remark (1935 : 103) that in his experience " the habits of these two races or species are so different that treating them as distinct species . . . is a great convenience " should be noted; but it is unlikely that they are more than geographical races.

chambers, consisting of air-tight vessels, were made up with various strengths of potash and the flies were kept in them in containers.

As regards food, the flies in 1934 were fed on a sheep, daily unless otherwise stated. In Potts's earlier experiments (1933 : 294) " there was a suggestion that cattle blood was more suitable than that of goats, as the female mortality was significantly higher amongst the flies fed on this blood, although the numbers of larvae produced were not significantly different." This is in line with observations by myself (quoted by Nash, 1930 : 241).

For the selection of pupae, Potts evolved " buoyancy " tests by means of which the living, dead and parasitised pupae could be separated from a miscellaneous collection. Pupae are first immersed in methylated spirit; those pupae that sink may be considered to be alive; then those that have floated are immersed in petrol; the pupae which then sink may be considered as parasitised and those floating as dead. Brief immersion in these liquids did not affect the pupae adversely. It is useful further to note (as Buxton *in litt.* points out) that if one weighs pupae daily or frequently one can define the time of the occurrence of death.

4.—THE WEIGHTS OF WILD PUPAE COMPARED WITH THOSE OF LABORATORY-BRED PUPAE.

Laboratory-bred pupae were in each species several milligrams lighter than those found in the field. The weights of the latter were found to range from an average of 20·85 mg. in the case of *G. austeni* to averages of about 27 and 30 mg. in those of *G. swynnertoni* and *G. morsitans* respectively. Laboratory-bred pupae of the much larger *G. pallidipes* gave an average of about 31. The wild pupae of this species probably weigh several milligrams more.

5.—THE INDIRECT EFFECT ON PUPAE OF TEMPERATURE APPLIED TO THE MOTHER FLIES.

A definite effect was observed. About 80% of pupae from adults at 30° C. (86° F.) died, whereas about 30% of those from 24–28° C. (75–82° F.) died, and among thōse from adults at 24° C. (75° F.) there was a still lower death rate (Buxton & Lewis). Flies from pupae collected in the field in December were lighter than those from pupae collected in July–August, and it was suggested that they were offspring of a less favourable period (Potts).

6.—THE MORE DIRECT EFFECT OF TEMPERATURE ON PUPAE.

(a) The effect on the pupal period of differing mean temperatures.

It is well known that the duration of the pupal period in *Glossina* varies as the temperature; low temperature, long pupal period; high temperature, short pupal period—Bruce and collaborators (1915), Lamborn (1916), Ll. Lloyd (1912*a* and *b*, 1914), J. K. Chorley (1929)—all *G. morsitans*; Harris (1930)—*G. pallidipes*; myself (1921)—observations on wild pupae of *G. morsitans* and *G. pallidipes*; Nash (1933*a*)—*G. morsitans*; Potts in Kikore (1933)—*G. morsitans*; Buxton & Lewis (1934)—*G. submorsitans* and *G. tachinoides*; and once more Potts—for the four species referred to below. The three last-named workers, with apparatus wherewith to obtain constant temperatures, confirmed the conclusions that earlier observers had arrived at. The effect of temperature is of importance as helping to understand the fluctuations in the numbers of the tsetses at different periods of the year.

Potts obtained the following results in his experiments :—

(i) With *G. morsitans* in Kikore the mean periods occurred of 30·9 to 48·5 days at different times of year, whilst during June and July in Sambala (a very cold period) one wild pupa took as long as 72 days to develop when brought into the laboratory. He found that a temperature of 30° C. (86° F.) lowered the mean pupal period (19 pupae) to 23·1 days as against 45·5 days in the control at room temperature. The latter varied from 66° F. minimum to 75° F. maximum (monthly means). The deaths at the higher temperature (see " c " below for details) were doubled.

(ii) With *G. morsitans* in 1934 in Shinyanga the pupal period varied from 33·9 days at 75·5° F. to 22·3 days at 82·4° F.

(iii) With *G. swynnertoni* the pupal period varied in his Shinyanga experiments from 35·5 days at 73·8° F. to 22·8 days at 82·4° F. As low a pupal period as 20 days was recorded at 87·8° F., but none of the flies emerging was strong enough to survive more than a few days. It is probable that about 22 days is the shortest period of pupal development that permits the production of healthy flies.

(iv) With *G. pallidipes*, pupal development varied from 25·9 days (female) at 72·3° F. to 36·6 days (males) at 74·4° F.

Two of Jackson's pupae marked in the field lay for 92 days before emergence. From 20 days to three months may therefore be taken as the range of the pupal period that may be produced by varying temperatures as ascertained by us up to the present.

The diurnal range did not appear to affect the rate of pupal development, which depended on the mean temperature to which the pupae were exposed. Series of experiments were carried out on *G. swynnertoni* (1) at varying temperatures, humidity not controlled, (2) at varying temperatures and constant humidity,* and (3) at constant temperatures and constant humidities.

An interesting point that emerged from series (1) was that the size of diurnal range of the temperature would appear to have little or no effect on the rate of development of the pupae.† Thus a mean daily temperature of 74·5° F. with a daily range of only 1·1° F. gives very nearly the same pupal period as does a mean temperature of 74·9° F. with a range of 14·1° F., or a mean temperature of 74·6° F. with a range of 22·6° F. (31·3, 32·5 and 31·7 days respectively). In brief, between 73·8° F. and 78·7° F. the pupal period falls from 35·5 days to 24·9 days.

The second series served as a check on the use of potash in humidity control. The third suggested certain conclusions which are dealt with elsewhere below and showed that " the temperature of 87·8° F. can be regarded as practically lethal for the species (if maintained continuously, which of course it never is under natural conditions), since not one of the emerged flies from this series of experiments ever survived to feed twice, and many were not strong enough to feed once " (Potts, report 1934).

On the information available we may thus conclude generally that too high a mean temperature produces two adverse effects : (i) it kills a greater proportion of the pupae than do lower temperatures; (ii) it affects the size and also the viability of the flies that actually emerge.

*** This is relative humidity. With rising temperature and constant relative humidity, saturation deficit, of course, increases.**

† Later statistical treatment of the figures has shown that a greater diurnal range does lessen slightly the rate of pupal development, but that this effect, which appears more marked at lower mean temperatures, is small, a matter of one and a half days at the most.

(b) The lethal effect of short exposures to high temperatures.

Potts found that with the pupae of *G. swynnertoni* exposures to 102–104° F. of from ½ to 2 hours did not interfere with pupal development, but that exposure for 3 hours greatly diminished the number of flies emerging. Exposures to 111–113° F. of over half an hour were lethal.

He also found with the pupae of *G. morsitans*, (α) that even 40° C. (104° F.) was lethal when continued for 4 hours or more; (β) that 45–50° C. (113–122° F.) killed in half an hour; and (γ) that whilst pupae can survive an exposure of 2 minutes to 55–57° C. (131–134·6° F.), the lethal temperature of exposures of 5 minutes lies between these two temperatures and for exposures of 15 minutes between 50° and 55° C. Thus both degree of temperature and length of exposure contributed to the effect on the pupae.

"The upper thermal death-point was not far from that of the adult" (Buxton & Lewis, 1934). Nash (*see* p. 182 below) had concluded that 112–113° F. was the death-point. Buxton and Lewis's pupae of *G. submorsitans*, 15 days old, survived at 111·2° but not at 113°. Near the beginning and end of pupal life they succumbed at 109·4°.

Potts drew attention to the fact that in Shinyanga a surface soil thermometer in an exposed site without cover, read at 2 p.m., registers a monthly mean temperature of over 111° F. for many months in the year, and over 102° F. for all the year except December to February, and that pupae deposited outside the normal sheltered sites, or deprived of such shelter, would therefore stand little chance of survival during the greater part of the year. Buxton and Lewis drew a similar inference from the conditions which they studied in Nigeria: "It is possible that in the hot dry months the mean temperature in the soil, even in the densest shade, may be sufficiently high to cause the death of many puparia, and that even a very little clearing might cause a great increase in these deaths" (1934 : 228). I have myself recorded (Swynnerton, 1923 : 119) a high proportion of dead among a number of pupae of *G. morsitans* and *G. pallidipes* that had been naturally deposited in open sites. Nash and Lloyd proved experimentally in the field that mortality due to this can take place. Fuller and more varied observations than have yet been carried out on soil-temperatures at one inch will be useful.

(c) The effect of longer exposures to high temperatures.

Of nineteen puparia kept by Potts constantly and continuously at 30° and 35° C. (86° and 95° F.) three-quarters completed their development at 30° C. (86° F.) in a much shorter time than the control, but the mortality was 26·3% —*i.e.* double that of the control (13%)—the latter having been kept at 19–24° C. (66–75° F.). They could not, however, complete their development at 35° C. (95° F.). Thirteen puparia kept at this last temperature all failed to survive 13 days.

Buxton and Lewis found that both in *G. tachinoides* and *G. submorsitans* the mortality is higher at 30° C. (86° F.) than at 24° C. (75° F.), even at the most favourable humidity. "24° C. (75° F.) may therefore lie in the region of the optimum temperature, while there is increased mortality at either higher or lower temperature."

(d) The effect of exposures to very low temperatures.

Potts found by experiment that on exposure of pupae of *G. morsitans* to 0° C. (32° F.) for as long as 24 hours 66% emerged as compared with 84% of the control. The figures were not very significant (the observed difference

between treated and control pupae would occur by chance between 1 in 10 and 1 in 20 times), but exposure for from 1 to 1½ hours definitely did not affect the percentage emerging (96 and 97% as opposed to 89 and 96% in the controls).

(e) The effect of exposing pupae to intermittently varying temperatures.

In nature pupae of *G. morsitans* under savanna conditions are subjected to temperatures that must often vary widely within the 24 hours, as observations by myself (Swynnerton, 1921) and (with readings) by Jackson suggest. It seemed possible that a pupa might stand occasional exposures to otherwise lethal temperatures if these were alternated with lower temperatures for longer spells. Potts actually found of *G. morsitans* that whereas (as stated already) pupae were " unable to withstand 40° C. (104° F.) for much over four hours, they could withstand longer periods than this, even up to ten or twelve hours, if the exposures were administered in daily doses of two hours, or possibly even of four hours " (Potts, 1933 : 298).

7.—THE EFFECT OF DEPRIVING PUPAE IN THE FIELD OF THEIR NATURAL SHADING.

My observation (1923) on this subject has been referred to sufficiently already. Herbert Lloyd carried out the following experiments on *G. morsitans* at Kikore in August of 1924.

" 1. Placed in ' bad ' sites.

" (*a*) Under light canopy of but away from the trunks of *Isoberlinia globiflora*.

Emerged	251
Died in puparium	5
Eaten by predators . . .	3
Percentage emergence . . .	97%

" The trees were mainly leafless during the period but there was a thin carpet of leaves to insulate the soil from the sun's rays and prevent it from becoming heated to a temperature lethal to tsetse pupae. It is probable, though at present untested, that when there are few leaves on the ground but the *Isoberlinia* is in full leaf, the mere canopy of the trees would act as a sufficient heat insulator.

" (*b*) Under light canopy of *Brachystegia microphylla* but away from the trunks. Here again leaf-fall set in and the same remarks apply as to the previous paragraph.

Emerged	136
Died in puparium	55
Eaten by predators . . .	4
Percentage emergence . . .	70%

" (*c*) In an open grassless clearing of *Isoberlinia globiflora*. The site was exposed to the direct rays of the sun and had no carpet of leaves on it.

Emerged	2
Died in puparium	366
Percentage emergence . . .	0·5%

" As would be expected the position was entirely unfavourable. The two pupae that gave rise to flies must have done so within a few hours of burial.

"2. A control was chosen in the *Isoberlinia* wooding where the pupae were placed under a log of large dimensions.

Emerged	355
Eaten by predators	14
Died in puparium	1
Percentage emerged	96%

"The loss here due to predators would appear to be larger than in the more open places.

"These figures need no comment but emphasise the need for the repetition of the experiment at other times of the year and in other situations" (H. M. Lloyd, report).

Nash (1933*a* : 181) carried out a number of experiments in which tsetse pupae (*G. morsitans*) were exposed for a day on the surface of the soil with a maximum recording thermometer. The experiments showed that if the sun temperature at the surface of the soil reached 113° F., all the pupae would be killed.

The next step was to discover to what depths the sun could raise the soil temperature to the level required to destroy the puparia, taking into account the season of the year. The effect on the Bombyliid parasite, *Thyridanthrax*, found in some of the tsetse pupae, was noted also.

(a) Exposure during the cooler parts of the year (late July).

Nash has recorded that during the cooler parts of the year (late July) in Kikore "over a period of five days four batches of 50 pupae were exposed to the following conditions:—One batch was placed on the surface of the soil, and the other three batches were buried under half, one, and two inches of earth. A fifth batch was kept in the laboratory as a control. A maximum recording thermometer was placed with each batch at the same level as the pupae. At the end of the fifth day the pupae were removed, placed in the laboratory, and the subsequent emergences recorded." The results are given in table 31 below.

TABLE 31.

The effect of depriving pupae, buried at different depths, of their natural shading in the field for five days in July.

Depth	Max. temp. for period (F.)	Mean max. temp. for period (F.)	Emergences during exposure	Emergences after exposure		Total emergence % (parasites included)
				Tsetse	*Thyridanthrax*	
Surface	140·50	130·00	5	0	0	10
½ inch	133·50	121·50	4	0	0	8
1 inch	118·00	110·50	4	0	3	14
2 inches	110·00	103·00	10	30	3	86
Controls	76·00	74·00	5	33	4	84

"The pupae were exposed at dawn on an overcast morning; when the sun came out and the soil started to warm up, the heat caused an acceleration in emergence. All the emergences down to the one-inch depth, recorded in column 4 as having taken place during the five days' exposure period, actually

took place before 11 a.m. on the first day. A separate experiment has shown that unless the initial exposure is made in hot sun near midday quite a number of tsetse will escape the lethal effects of the sun. A comparison with the laboratory controls shows that the number of emergences on the first day is much greater with exposed pupae; a definite acceleration takes place, the emergence being advanced by as much as four days. Hence the figures for exposures from the surface down to one inch, as given in column 4 and in the last column, do not mean that flies survived the first day's maximum temperature; they are all based on the initial emergence that took place during the first few hours of the exposure. It will be seen from the emergences *after* the five days of exposure (column 5), that all tsetse down to one-inch depth were unable to survive the maximum temperature of 118° F. recorded at this level; however, the *Thyridanthrax* were unaffected. At two-inches depth pupae of *G. morsitans* were not killed by the maximum temperature of 110° F.; they were as healthy as the controls."

(b) Exposure during the warmer parts of the year.

Nash carried out a similar experiment in the warmer weather of September. The pupae were not exposed until midday, in order to prevent the escape of a few tsetse owing to accelerated emergence. The results are given in table 32. The basis adopted is identical with that in table 31 with the one exception that a depth of one and a half inches was substituted for two inches.

TABLE 32.

The effect of exposing pupae in the field in September.

Depth	Max. temp. for period (F.)	Mean max. temp. for period (F.)	Emergences during exposure	Emergences after exposure		Total emergence % (parasites included)
				Tsetse	*Thyridanthrax*	
Surface . .	154·50	142·00	0	0	0	0
½ inch . .	147·00	135·00	0	0	0	0
1 inch . .	125·50	120·00	0	0	0	0
1½ inch . .	119·00	112·00	0	0	2	4
Controls .	76·00	74·00	5	33	4	84

"It will be seen from column 5 that all pupae of *G. morsitans* were killed down to a depth of one and a half inches, being unable to withstand a maximum temperature of 119° F.; however, *Thyridanthrax* was unaffected. Owing to the initial exposure being made in hot sun near midday there were no emergences during the five days (column 4); all pupae were probably killed very shortly after exposure. Many further experiments have proved that, except during the rains and cold weather, an exposure of one day is quite sufficient to kill the tsetse pupae. The maximum temperature at one and a half inches during a day is usually about 118° F., and as tsetse pupae are killed at about 112° F., there is quite a margin of safety" (Nash).

From a third series of experiments, which need not be so fully quoted, "it was concluded that during the rains at least three consecutive fine days are required to destroy the tsetse pupae; even if these occur a few fly will successfully emerge in the first two days, when the soil is so wet that high temperatures are impossible."

(c) Conclusions.

The results were very promising. " It was concluded that the exposure, during the dry season, of the breeding-sites of *G. morsitans* to the midday sun would result in the destruction of all tsetse pupae down to a depth of at least one and a half inches. Since pupae are rarely found at depths exceeding half to one inch, it was clear that very few pupae would ever escape destruction. The same holds good for the cold season. During the rains results were not quite so satisfactory " (Nash, 1933*a* : 182–184).

" The thermal death-point of *submorsitans* puparia exposed on the 15th day is the same as that found by Nash for puparia exposed for a day on the surface of the soil (Nash, 1933*a* : 181). All puparia were killed when the maximum temperature of the soil rose to 45° C. (113·0° F.) during some part of the day " (Buxton & Lewis, 1934 : 213).

8.—THE EFFECT OF HUMIDITY ON THE DURATION OF THE PERIOD OF PUPAL DEVELOPMENT AND ON THE MORTALITY OF PUPAE.

Potts did not find that in general differing humidity affected the duration of pupal development. This was dependent on temperature alone. He found that mortality was affected by humidity as stated in (9) below.

Buxton and Lewis (1934 : 235) found that " humidity has no effect on the duration of life but much on the mortality, the optimum being at or near saturation at least for *tachinoides*." At 37° C. (98·6° F.) and a high relative humidity (80%) no pupae lived more than a few days. With *G. tachinoides* at 30° C. (86° F.) the survival rate steadily fell with decreasing humidity. The differential effect of factors on different species of tsetse was illustrated by the fact that both temperature and humidity caused greater differences in mortality in pupae of *G. tachinoides* than in those of *G. submorsitans*. In the latter there appeared to be no relation between survival and humidity except at the very low relative humidity of 11% at 30° C. (86° F.). Pomeroy and Morris (1932) have stated that " the length of the pupal period is markedly affected by atmospheric humidity so that pupae deposited early in the dry season and those deposited later all appear to hatch out at about the same time "—at the outset of the first rains. Buxton and Lewis's work went to disprove this explanation. A similar " rush " effect observed by myself in Portuguese East Africa in the late season in numerous pupae of *G. morsitans* and *G. pallidipes*, deposited early and late, coincided with rising temperature without rain. Buxton and Lewis suggested that the atmosphere in the soil is in any case nearly saturated owing to diffusion of water vapour from below, and that this is so, even when no rain has fallen for months and when atmospheric humidity is very low. This view Herbert Lloyd confirmed as regards humus by measurements of humidity in the humus layer that contained the pupae on Riamugasire Island.*

9.—THE EFFECT OF TEMPERATURE AND HUMIDITY AT DIFFERENT STAGES IN THE PUPAL LIFE.

Potts found in his experiments on the pupae of *G. swynnertoni* that shortly after deposition they may be much more susceptible to the adverse effect of abnormally high temperatures than older pupae. It was suggested by other figures that pupae nearing their emergence time may similarly be specially

* Lloyd used a hygrometer of cellophane, pleated and pushed into a specimen tube. There was probably some inaccuracy, but there seemed at any rate to be no doubt that the relative humidity ranged between 80% and 100%. Buxton (who first suggested the method) used paper.

susceptible to adverse effects. He also concluded that " towards the lethal end of the temperature scale extreme humidities, either wet or dry, minimised the chances of the pupa giving rise to an adult fly." Buxton and Lewis also found that adverse influences generally were more effective at the beginning and end of the pupal period.

10.—THE EFFECT OF TEMPERATURE AND HUMIDITY ON THE WEIGHT OF PUPAE.

Buxton and Lewis found that humidity affects the loss of weight and that more weight is lost at low than at high humidities. The loss at 24° C. (75° F.) in pupae of *G. submorsitans* ranged from 7·8% to 21·3% of the original weight. Except at high humidities it was almost proportional to saturation deficiency and was therefore due to evaporation. More weight was lost at 24° C. (75° F.) than at 30° C. (86° F.). This was shown to be due to the greater duration of pupal life at the lower temperature. *G. submorsitans* loses less weight per cent. per day than does *G. tachinoides*.

" Under natural conditions there may be a high mortality if the temperature is low and the air in the soil is not saturated; the pupal period may be extended, for example, to 50 days or more " (Nash, 1933); and throughout the period (Buxton and Lewis) the weight steadily continues to diminish—with the risks referred to below.

Buxton and Lewis found that nearly all the dry material lost was fat, which is used to meet the needs of the developing adult—more than half of it being used—while (as already stated) the loss of weight consisted almost entirely of water. " The puparium does not compensate for high evaporation by burning fat."

11.—NORMAL LOSS OF WEIGHT DURING THE PUPAL PERIOD, AND ITS RESULTS.

Potts found that pupae of *G. morsitans* were heaviest just after deposition and that thereafter they lost weight gradually until their emergence to a total of between 2 and 4 milligrams. It was found that pupae which weighed under 15 milligrams were not worth including in the experiments, as they rarely if ever gave rise to an imago even when kept under favourable conditions.

The longer the pupal period, therefore, the greater the chances of death of the pupae themselves and of the weakened flies that emerge from them—through gradual loss of weight. The longer the period, also, the more prolonged the exposure to risks generally.

12.—THE EFFECT ON PUPAE OF INUNDATION AND WATER-LOGGED SOIL.

" Batches of ten puparia were placed in water for periods varying from one hour to fourteen days. . . . A submergence of up to four days is not fatal to tsetse pupae; above four days it is fatal in every instance " (Nash, 1933*a*: 114).

Nash buried " two batches of twenty-five pupae at one inch depth in two tins, that were filled with water-logged soil. No single pupa produced a tsetse either during the first five days or afterwards. It can be concluded that the pupae of *G. morsitans* cannot survive inundation or exposure to water-logged soil conditions for more than four days."

" Burial of pupae in sand saturated with water, or covering them entirely with shellac, proved fatal (100% mortality) " (Potts, 1933).

Buxton and Lewis (1934) found that immersion in water for shorter periods

than Nash's killed their pupae. They suggested that this was partly due to the fact that these were only from 0–5 days old at the time of exposure, for they found that pupae in middle life live longest under submergence. They found that "... submergence in water-logged soil for 24 hours or more is fatal for all *tachinoides* puparia. ... There is apparently no important difference between *tachinoides* and *submorsitans*" (Buxton & Lewis, 1934 : 215).

13.—THE EFFECT OF OCCLUSION OF THE SO-CALLED RESPIRATORY LOBES.

Potts found that "occlusion of the respiratory lobes alone, with shellac, was not fatal, nor was the application of a similar patch of shellac to the anterior end" (Potts, 1933 : 298).

14.—DIFFERENCE BETWEEN THE PUPAL PERIOD OF MALES AND FEMALES.

The males of *G. morsitans* took longer to complete their pupal period than did the females, their average period in Potts's experiments in Kikore being 47·2 days, and at Shinyanga 29·8 days, as compared with 43·0 and 28·1, respectively for the females. Ll. Lloyd (1913 : 286) working with the same species in Northern Rhodesia, found a similar difference, as did Buxton and Lewis working with *G. tachinoides* and *G. submorsitans*. *G. swynnertoni*, also experimented with by Potts in Shinyanga, showed the same average periods as *G. morsitans* for males and females respectively. The average pupal period of *G. pallidipes* under the same conditions was from two to three days longer in the males than in the females.

15.—SUMMARY OF THE CONDITIONS LETHAL TO PUPAE.

"The only conditions encountered under which all puparia die are a rise of temperature to the thermal death point [113° F.] and subjection to prolonged submergence ... the extent of mortality depending on the degree of severity [of the adverse conditions], the age of the puparia and their previous history" (Buxton & Lewis, 1934 : 217).

16.—OBSERVATIONS ON PARASITES MADE IN THE COURSE OF THE EXPERIMENTS.

One species of Hymenopterous and three species of Dipterous (Bombyliid) parasite were bred from these tsetse pupae by Potts. The Hymenopterous parasite (*Syntomosphyrum glossinae* Waterst.) was scarce in nature; *e.g.* in a series of 2,185 pupae, four only were parasitised (*i.e.* less than 0·2%). The Bombyliids were more numerous, *e.g.* of 2,724 pupae, 6·2% were parasitised.

The three species of Bombyliids were *Thyridanthrax abruptus* Lw. (the most common), *T. lineus* Lw., and *T. argentifrons* Aust. The last had previously been recorded only from west Africa.

Nash's experiments in Kikore on the effect of the sun on tsetse pupae on and in the soil produced interesting results as regards two of the puparial parasites, viz. *Thyridanthrax abruptus* and *Syntomosphyrum glossinae*. These suggested that *S. glossinae*, like the tsetse, cannot survive a maximum soil temperature of 113° F.; but that *Thyridanthrax* can remain unaffected by a soil temperature of 119° F. "The fact that these parasites can withstand greater temperatures than *G. morsitans* is important, as it will mean that when all tsetse and *S. glossinae* are destroyed by the sun, a few *Thyridanthrax* will survive. Thus one will tend to increase the proportion of these parasites in the bush" (Nash, 1933*a* : 185).

17.—THE EFFECT OF TEMPERATURE ON ADULT FLIES.

(a) The effect of exposing adult flies to constant high temperatures.

Potts working with *G. morsitans* (1933) found that adult flies failed to withstand exposures of as much as one hour to 40° C. (104° F.).

Buxton and Lewis working with *G. tachinoides* and *G. submorsitans* (1934 : 225) found that an hour's exposure to 43° C. (109·4° F.) was critical and 44° C. (111·2° F.) fatal. On a three hours' exposure 40° C. (104° F.) killed some flies and 40·4° C. (104·7° F.) killed all. They noted that during March, April and in May at Gadau the screen temperature outside frequently passed 38° C. (100·4° F.) and even 40° C. (104° F.). "At 44% and 11% humidity, *submorsitans* lives almost twice as long as *tachinoides*. . . . Under conditions of constant high humidity, at 30° C., both species died out quickly" (Buxton & Lewis, 1934 : 233).*

(b) The effect of exposing adult flies to intermittent high temperatures.

Adult flies survived short exposures to 40° C. (104° F.) even when repeated a number of times. Buxton and Lewis noted that the temperature recorded in the field was frequently high enough and for periods sufficient to kill *Glossina* in open country or partial shelter, but not in the thickest places. They concluded that, unless it has continual access to water, perhaps in the form of blood, by evaporating which it could lower its body temperature, *Glossina* probably avoided continuous exposure to heat by resorting for short periods to places where the temperature is lower. This intermittent retirement was suggested by myself also, from field observations (1921 : 360).

(c) The effect of exposing adult flies to low temperatures.

Potts (1933) found that adult flies recovered from exposures to 0° C. (32° F.) of three to twelve hours' duration, although it was suggested that their ability to digest blood may have been impaired. In Buxton and Lewis's experiments, after exposure for from seven to ten minutes to 0° C. many flies became ataxic and died in a day or two; a few recovered after a period of from 4 to 7 hours. Exposure to 12° C. (10·4° F.) for from seven to ten minutes killed every time.

(d) The observed effect of temperature on flies in the field.

Nash showed that a regular reduction in fly density takes place at Kikore during the annual cold spell (1933*a* : 118). He believed that the cold killed the old flies, as the young fly figures remained high. Generally, Nash concluded (1933*a* and *b*), from his four years of very thorough work on the effect of the meteorological factors on the flies in the field, that in the density figure month by month there appears no correlation between *G. morsitans* and temperature in the same month or previous month, but that with the temperature of two months previous there is a very small but just significant correlation. Temperature is really only important, he considered, in so much as it influences the evaporating power, or the saturation deficiency, of the atmosphere. Temperature alone plays but little part in determining the seasonal variations in fly density. It is the combination of temperature and humidity, no matter whether in the form of evaporation or saturation deficiency, that is of vital importance in controlling the numbers of tsetse. But it should be noted that Nash's air temperatures, in Kikore, were seldom lethal, as shade temperatures

* Buxton informs me that this effect of high humidity requires to be confirmed. It may have been due to some toxic material, given off when rubber washers of a type which he used are left in contact with moist air (*see* Buxton & Mellanby, 1935).

often are *per se* in Nigeria. Nash's own valuable recent paper on this last subject should be seen (Nash, 1935).

18.—THE EFFECT OF HUMIDITY ON ADULT FLIES FED ON THE BLOOD OF SHEEP.

(a) Mortality and feeding.

Potts's experiments in 1934 were disappointing in that the mortality of the flies was higher and the production of pupae lower than would have been compatible with the survival of the species in nature. Also, the humidities under which *G. morsitans* and *G. swynnertoni* respectively did best, as regards mean life of flies living over ten days at any rate, were the reverse (as between the two species compared) of what the field-observations would have led one to expect. The mean life of such individuals of *G. morsitans* as survived over 10 days was at the best 38·1 days, and that at the lowest humidity (20%); on the other hand, the mean life of *G. swynnertoni* was longest (26·2 days) at 90% relative humidity. The question arose whether each time there is an inspection of the jars a lowering of the humidity takes place sufficient to vitiate the observations (Potts).

Mortality in Buxton and Lewis's experiments on *G. submorsitans* was higher at 88% humidity, but in this connection the footnote on p. 187 should be consulted. At the lowest humidity, 11%, the proportion of nil feeds was high—39·5%. " At intermediate humidities the flies fed nearly every day. At 30° C. and moderate humidity (44%) the two species of *Glossina* live longest, eat most and have the highest birth-rate " (Buxton & Lewis). Nash found in his field work in Kikore that a moderate evaporation was associated with higher fly counts.

(b) Reproduction.

Potts found that both *G. morsitans* and *G. swynnertoni* produced more pupae at 20% relative humidity than at any of the higher humidities. Buxton and Lewis found that *G. submorsitans* produced more pupae at a relative humidity of 11% than at 44%. At 88% humidity, no reproduction occurred. At 44% humidity reproduction was active. It seemed clear, they concluded, that the most favourable humidity for *G. submorsitans* of the humidities tested was 11%. It will be recalled that Johnson and Ll. Lloyd found 20–40% of *G. tachinoides* pregnant in the rains, 80% in the dry season.

Field observation on pupae strongly confirms these conclusions, both on *G. swynnertoni* (observations by Potts) and *G. morsitans* (observations by Jackson).

(c) Some details of the experiments carried out by Potts.

(i) *Experiments on* G. morsitans.

TABLE 33.

Length of life of *G. morsitans* kept in large glass jars, and number of pupae produced by such flies, fed daily on the blood of sheep and kept at different relative humidities.

% relative humidity	Number of flies	% living over 10 days	Mean life of those living over 10 days	Maximum life of females	Total females living over 10 days	Pupae produced	Pupae per female per 20 days
20	30	53	38·1	65	11	5	0·21
60	30	70	31·1	63	13	4	0·14
90	35	46	28·6	55	11	1	0·06
100	60	57	23·0	46	23	3	0·11

TABLE 34.

Length of life of *G. morsitans* kept in brass rings,* and number of pupae produced by such flies fed daily on the blood of sheep and kept at different relative humidities.

% relative humidity	Number of flies	% living over 10 days	Mean life of those living over 10 days	Maximum life of females	Total females living over 10 days	Pupae produced	Pupae per female per 20 days
20	25	52	30·8	61	9	3	0·20
60	23	52	22·6	40	12	0	0·00

* These rings were about ¾ inch deep and 2 inches in diameter, closed with gauze above and below.

From these tables it would appear (i) that the larger containers were slightly more suitable for maintaining the flies alive; (ii) that as regards mean length of life, there was a slight but steady increase with decreasing relative humidity, 20% being apparently the most favourable; but (iii) that as regards survival for more than 10 days the results were less clear-cut: 60% being, apparently, much more favourable than 20%, 90% or 100%, though even at the last named humidity 57% of the flies lived more than 10 days; and (iv) that few pupae were produced compared with the normal expectation of at least 1 per female per 20 days. In this case, as in that of the length of life, 20% seemed the most favourable. It is interesting and a little unexpected that the flies should produce pupae at all at 100%.

In view of the possibility that there might be an optimal zone between 20% and 60%, a jar was started at 40% humidity, but did not produce startling results.

Note.—An error is suspected in the case of these experiments with large jars. It is probable that when they are taken out of the humidity chambers the air therein became mixed with the outside air and probably took some time to return to the supposed humidity. Thus the alleged 100% and 90% relative humidities were possibly not so high, and the alleged 20% was probably not so low. The 60% was probably not very much altered.

(ii) *Experiments on* G. swynnertoni.

TABLE 35.

Length of life of *G. swynnertoni* fed daily on sheep and kept at different relative humidities in brass rings.

% relative humidity	Number of flies	% living over 10 days	Mean life of those living over 10 days	Maximum life of females	Total females living over 10 days	Pupae produced	Pupae per female per 20 days
20	31	45	22·3	40	9	1	0·10
60	28	75	24·6	42	16	1	0·05
90	54	65	26·2	78	26	3	0·08
100	51	45	22·1	49	23	1	0·04

These flies (*G. swynnertoni*) were all kept in brass rings, and this may account for the figures being rather lower than those obtained for *G. morsitans*.

There is little difference between the mean life of the flies that lived more than 10 days—the difference being only that between 22·3 and 26·2 days. The percentage of flies living over 10 days was highest at 60%, though the number of survivors (both sexes taken together) at 90% was surprising considering the indications from field-observation. (See note just above.)

The number of females surviving at one or other of the two highest temperatures (23 female *G. morsitans* at 100% relative humidity, and 26 and 23 female *G. swynnertoni* at 90 and 100% relative humidity respectively) is very high in both species. Females, it may be recalled, seek in nature more secluded eco-climates—such as in fact might be called "ecidio-climates"—than males and their tolerance for higher humidities may be greater. Unfortunately the experiments on the two species are not strictly comparable, no *G. morsitans* having been kept in the brass rings at the highest humidities, while no *G. swynnertoni* were kept in jars.

The above experiments were all carried out in the incubator room, the monthly mean temperature rising from 73·6° F. in August to 78·3° F. in September and 77·1° F. in October. The sexes were maintained in the proportion of 5 males to 10 females in the large glass jars and of 2 males to 3 females in the brass rings. All were fed on sheep's blood.

(d) Some details of the experiments carried out by Buxton and Lewis.

In the case of *G. tachinoides* 44% humidity is near the optimum for feeding, longevity of females, and birth-rate. Lower humidities are less favourable in each respect. "Middle humidities are the most favourable, at any rate at 30° C. and higher temperatures; this is true of both species [*G. submorsitans* and *G. tachinoides*], and for fed and also unfed flies."

19.—SURVIVAL OF YOUNG ADULT FLIES WITH, AND WITHOUT, A MEAL AT DIFFERENT HUMIDITIES AND TEMPERATURES.

(a) Young adults of *G. morsitans*.

Potts carried out a series of experiments, involving 931 flies which emerged in the laboratory, to determine how long a fly could live without food (i) if it had never had a meal and (ii) if it had had one meal. Apart from their having a bearing on the probabilities of survival of young flies under different physical conditions in nature, these observations were also designed to serve as a basis for further experiments on the effect of the frequency of the meal on the general well-being of the fly. For actual survival in nature, the periods can be reduced by one day, since for the last day of life the flies were generally too weak to be able to feed, and would therefore have died in any case.

The sex proportions in which the flies were kept together had no effect on the period of survival. The period that a young fly was able to survive without feeding increased with a rising humidity and decreased with a rising temperature. The maximum mean survival period without feeding recorded was 6·1 days at 100% relative humidity and 73·5° F. The effect of a meal was to increase markedly the period of survival at low humidity, and slightly at medium and high humidities; at the same time, flies with a meal survived at high temperature combined with medium humidities.

(b) Young adults of *G. swynnertoni*.

A few figures only are available, as Potts experienced difficulty in getting pupae of this species in large numbers. However, from a total of 107 flies it

TABLE 36.

The survival of young flies with, and without, a meal under different conditions and in different sex proportions.

Conditions		5 males		4 males 1 female		3 males 2 females	
Temp.	R.H.	No. of flies	Mean life	No. of flies	Mean life	No. of flies	Mean life
73·5° F.	20%	20	3·1	20	2·9	20	3·0
,,	60%	21	5·5	20	4·6	20	4·9
,,	90%	20	7·1	20	5·7	20	5·3
,,	100%	20	5·5	20	6·1	20	5·5
87·8° F.	20%	20	1·9	—	—	20	1·5
,,	100%	20	2·9	20	3·3	20	2·9

Conditions		2 males 3 females		1 male 4 females		4 females	
Temp.	R.H.	No. of flies	Mean life	No. of flies	Mean life	No. of flies	Mean life
73·5° F.	20%	20	2·9	20	3·1	20	2·9
,,	60%	20	3·9	20	3·3	20	4·3
,,	90%	20	5·4	20	5·3	20	5·3
,,	100%	20	5·5	20	5·9	20	5·7
87·8° F.	20%	20	1·9	22	1·7	25	1·9
,,	100%	20	3·3	20	3·5	20	3·8

TABLE 37.

The effect of a meal on the survival of young flies (*G. morsitans*).

Relative humidity	Mean life at 77·7° F.	Mean life at 73·7° F.	Mean life at 87·8° F.	
	With meal*	Without meal	With meal	Without meal
20%	4·5 days	2·9–3·1 days	3·5 days	1·5–1·9 days
60%	4·8 ,,	3·3–5·5 ,,	4·2 ,,	—
90%	6·6 ,,	5·3–5·7† ,,	6·2 ,,	—
100%	6·7 ,,	5·5–6·1 ,,	3·4 ,,	2·9–3·8 days

* The meal in all cases was human blood.
† The aberrant figure from the preceding table has been omitted.

was found that the average length of life of unfed flies at 77·7° F. and 20% relative humidity was 2·3 days and that this increased only to 2·8 days at 60% relative humidity. After a meal, the figures were 4·4 days and 7·2 days respectively. Whilst the figures at 60% are surprisingly low compared with the other species, the mean survival at 87·8° F. and 100% relative humidity is surprisingly high (5·4 days). However, the figures need confirmation.

(c) Young adults of *G. austeni.*

Two batches of flies kept at 20% relative humidity and 77·7° F. gave a mean survival period of 2·3 days unfed and 2·5 days fed (on human blood), whilst two similar batches at 100% relative humidity at the same temperature each had a mean survival period of 7·7 days.

(d) Freshly emerged individuals of *G. tachinoides.*

Nash found that freshly emerged flies of this species with a meal have a greater resistance to high maximum temperatures than older flies (Nash, 1935 : 110).

20.—THE WEIGHT OF FLIES AND ITS IMPLICATION.

"Since the weight of pupae deposited in the laboratory seemed to be lower than that of 'wild' pupae [*see* p. 178 above], the weights of freshly emerged flies from laboratory pupae were compared with those from wild pupae. Twenty-five adults emerging from laboratory pupae averaged 12·0 mg., whilst the same number from wild pupae averaged 15·0 mg. This is slightly lower than the average of 16·5 milligrams based on eight young flies staged as young in the field during the same period, but the numbers are too small. It is interesting to note that this average of 16·5 mg. from eight wild young flies in December is again lower than that of 17·6 mg. from 21 young wild flies collected during July–August. By itself, the difference is small, but a similar and even greater difference was observed in all stages of flies collected during these two periods, so that some significance may be attached" (Potts : 1934). It was suggested (by Potts and Jackson) that the July–August series may be offspring of a more favourable period than those of the December series. This of course supports the general conception, based on more indirect lines of evidence, that the late dry season constitutes a hard time for the tsetse flies of the savanna.

Buxton and Lewis note, however, that high temperature produces light pupae, and it is possible that this may be the whole explanation of the lightness of flies emerging from pupae deposited at the end of the dry season.

21.—THE FAT AND WATER CONTENT OF FLIES.

In the course of the above weighings of the young flies reared in the laboratory it appeared that they became progressively lighter as the period after emergence increased, and that this loss in weight corresponded to a decreasing fat percentage. Incidentally, as may be seen from the table below, the fat percentage of the laboratory-bred flies is considerably below that of those emerging from wild pupae, whilst the water percentage is slightly but

TABLE 38.

Fat and water content of flies emerging from wild pupae and laboratory-bred pupae respectively.

Period after emergence	Under 1 day			4–5 days		
Flies emerging from	No. of flies	Water %	Fat %	No. of flies	Water %	Fat %
Wild pupae . . .	17	68·2	25·3	12	67·7	12·7
Laboratory-bred pupae .	12	70·5	15·9	6	69·8	9·8

consistently higher. This point will be discussed again when considering experiments on the feeding of flies.

"These insects possess the power of compensating for loss of water from the body, so that though one group (88% relative humidity) lost about 20% of its original weight during starvation, while another group (44% relative humidity) lost about 36%, the proportion of water in their bodies at the end of the experiment was hardly different. . . . This regulation is brought about by using fats. . . . *Glossina* is one of those insects which compensate for evaporation by metabolising fat and also producing additional water. It seems . . . that there is greater evaporation in drier air, and that the increased metabolism of fat is not [in all cases] sufficiently rapid to compensate for it. Insects use more fat in dry than in damp air. It is also known that *Glossina* can survive a higher temperature in dry than in moist air for an hour. . . . At high temperatures, water of metabolism is produced rapidly and accumulates in the tissues unless the evaporative power of the air is considerable; but at low temperatures the rate of metabolism, and therefore of production of water, is less, so that insects can live normally over a much greater range of humidity. But there is no evidence that this water-logging occurs in *Glossina*. . . ." (Buxton and Lewis on *G. submorsitans* and *G. tachinoides*.)

"Actually the proportion of water *does* vary with the hunger of the flies. But if the weight of the fat be subtracted from both wet and dry weights the proportion of water in the remainder is very constant at about 70%. It is higher, at about 72·5%, in flies which have not had their first meal. There is lately some evidence that starvation may lower slightly their percentage to about 68" (Jackson).

The hunger stages (p. 38) bear a relation to the fat content of the flies, stage ii having most and stage iv and young and female flies least. Weight can also be correlated with the hunger stages, and so, to some extent, can percentage of water in non-fatty body-weight (Jackson's results).

22.—OTHER POINTS NOTED BY BUXTON AND LEWIS.

Buxton and Lewis include amongst their results :—

(i) the fact that in the last months of the year pupae deposited in the laboratory were significantly lighter than those deposited in cooler months. This has an effect upon the size of the adults of the next generation and may have far-reaching consequences.

(ii) the fact that flies will die of inanition rather than feed at high humidities;

(iii) the discovery that temperature and conditions generally in the field in the south of Nigeria at the end of the dry season are close to the lethal, for adults and for pupae, and that they must kill considerable numbers;

(iv) the observation that if adults are kept at 30° C. the resulting pupae have a high mortality. In the area in which Buxton and Lewis worked, the mean temperature of many months is close to this figure.

23.—POSSIBLE LIMITATIONS TO LABORATORY WORK.

The rate of emergence was satisfactorily high (76·7%) at Shinyanga and (86·8%) at Kikore, as it should be in the laboratory. Here the great variations in conditions, local and seasonal, which in nature produce the very variable mortality observed in the pupae collected in the field (from 45·6 to 70·4%

at Kikore in batches that totalled 2,271 pupae) is specially guarded against, unless as a part of the experiments. There is evidence that the loss in the field varies, as one would expect, with the season.

Further, Potts did not find that the use of potash to control humidity appeared to affect the pupae injuriously. On the other hand, as regards size, Potts found that the pupae produced in the laboratory were very much smaller than those collected in the field, being some 5–6 mg. lighter in the case both of *G. morsitans* and of *G. swynnertoni*; also that adult flies that had emerged from wild pupae were heavier than those which had emerged from laboratory-bred pupae and had a slightly lower water content with a markedly higher fat content. This must give rise to caution as to the laboratory results—for " pupae of *G. swynnertoni* weighing under 15 milligrams seldom gave rise to an imago " and one cannot be certain that abnormally light pupae will give rise to flies that will be in every way normal. That the viability of the resulting flies may be affected was in fact suggested by certain of Potts's results. Still, down to the usual laboratory weight, the laboratory-deposited pupae seemed able to develop normally.

As regards the effect of food, the experiments on flies fed daily on the blood of a sheep " proved disappointing in that, though the longevity of some flies was good, a very large proportion died young, and only very few pupae were produced. Thus, allowing even so low a reproduction rate as one pupa per female per 20 days, the most favourable conditions have only produced a quarter of the pupae they should."

Jackson found that captive flies (*G. morsitans*) lost weight more rapidly than flies which he weighed, released, recaptured, and weighed again; that in captivity dryness did not reduce the amount of fat after one to two days, though it increased the loss of water; and that the fat cycle is otherwise abnormal in captivity, synthesis of fat from the food being small.

The following also may be quoted from Potts's report (December 1934):—
" It seems obvious from the . . . results that the conditions under which adult flies have been kept in the laboratory have not been as favourable as they are in nature, otherwise the fly would [in nature] speedily die out, for not only are too few pupae produced [in the laboratory], but also too many young flies die without feeding. The low rate of pupal production is not due to refusal to copulate; that act frequently occurred in the breeding receptacles.

" There seem to me to be three possible lines worth exploring (doubtless there are many more). (i) In view of the results of feeding fly on cheetah and man and guinea-pig blood, as well as upon sheep, it may be possible that the exact diet of tsetse fly is of greater importance than has been suspected. The fat deficiency of the flies emerging from pupae deposited in the laboratory is worth dwelling on here.*

" (ii) in spite of the fact that at Kikore more pupae appeared to result from keeping 5 females with 3 males than from allowing only an occasional male, it is possible that absolute exclusion of the males, once copulation has taken place, may be necessary for normal breeding to occur. This is rather supported by Herbert Lloyd, who tells me that at Kikoré he got pupae from nearly 70% of his *morsitans* females, who only had access to the males for the first few days of their life. If the blood of game animals does not give better results, this line is worth trying again.

" (iii) If neither of the preceding alternatives produce better results, then I think consideration must be given to the cramping effect inevitable in the

* I have always regarded this as probably of very great importance.

controlled experiments that have been tried so far. It must be remembered that other species on which such experiments have been carried out with greater success have been on the whole much less active insects, such as bed-bugs and comparatively immobile plant-suckers."

Buxton and Lewis suggest that "it is possible that exposure to stable conditions of temperature and humidity is unfavourable to *Glossina*."

While tsetses are easily kept and bred in captivity they do not in these conditions lead a normal life or behave normally. The activity of buzzing in a tube is so obviously connected with nervous disturbance that it cannot be said to replace the normal activities and "interests" of natural life. The enforced quiescence of a fly with its wings snipped off equally cannot represent them. And it is in fact found that the digestive routine of the flies is very different from that of flies in the wild state. It has been noted already that Potts in his humidity experiments on adult flies fed on a sheep found that they were disappointing in that the mortality of the flies was higher and the production of pupae lower than would have been compatible with the survival of the species. Further, as Buxton and Lewis—also Potts—have suggested, it may be that exposure to stable conditions of temperatures and humidity is unfavourable to the flies, which in nature can ring the changes and have always the bush to retire to and the nights, with their greater humidity, in which to recuperate.

More work is therefore necessary before we can definitely say of an insect that is naturally so active, so selective probably of its food, and so selective as well of its environment from hour to hour, that the results obtained under conditions of close confinement, prescribed food and omission of various factors that the laboratory cannot provide, are in every respect reliable. At the same time a number of the results in the field and laboratory support each other, many of the results obtained offer definitely useful suggestions, and this method of investigation, on which Buxton has done so much, will undoubtedly give us—and in fact has given us—important clues to the explanation of phenomena in the field. These clues must themselves be examined in the light of the field observations. Jackson, who is very greatly impressed with the value of this type of laboratory work, says (in a recent letter to me), "I agree with Buxton that . . . suggestions should come from the laboratory first and then be tested in the field in so far as this is practicable, but I would not accept any laboratory finding unreservedly by itself." Buxton and Lewis have themselves observed that "detailed studies under controlled conditions in the laboratory mean little unless they are considered in relation to the insect's natural life."

P.—THE TSETSE FLIES IN RELATION TO THEIR FOOD.

1.—THE WORK SO FAR DONE BY THE TSETSE RESEARCH DEPARTMENT, TANGANYIKA TERRITORY.

Food-control and cover-control are the two ways in which we may attack the several tsetses indirectly. To put either method into effect economically as regards effort and as regards sacrifice of life or of vegetation, we must study thoroughly the habits of each species of tsetse in relation to it.

We have had time to attempt little work in the past on the relations of these blood-predators to individual species of animals—as regards their preferences and the bloods that best suit them. This work is only in its early phase, but the initial indications promise most interesting results.

A great deal of careful work has, however, been done on the habits and movements of *G. morsitans* in particular, and also on those of *G. swynnertoni*,

in relation to food animals in the aggregate. Jackson (with collaboration in the laboratory by Potts) has made the very full study of the hunger of *G. morsitans* and *G. swynnertoni* referred to on pp. 38 and 71 above, its diagnosis, its causes and implications. With the game under constant observation, he released more than 10,000 marked flies to note their subsequent movements in relation to feeding-grounds, and recaptured about 1,750. In other connections, he released twice as many. Nash in his work on the ecology of *G. morsitans* made a study of the effects of game-distribution and game-migration. Both have studied the general feeding habits of this fly. Burtt included in his study of *G. morsitans* at Sambala observations on that fly at particular water-holes that were (*a*) visited and (*b*) unvisited by game, and for two years he investigated the relation of game and *G. morsitans* respectively to dense thicket country. Moggridge studied the movements of *G. swynnertoni* to, and upon, animals in open country. Lloyd made observations on the feeding of tsetse on crocodiles.

2.—THE FOOD AND DRINK OF THE TSETSES.

(a) Experiments with the juices of plants.

It has long been known that certain flagellates—*Leptomonas* (*Phytomonas*)—that are closely related to trypanosomes are found in the milky juices of numerous species of plants and that part of their life is spent in plant-sucking insects, such as plant-bugs. It was, however, claimed recently by Mr. Davidson, of Natal, that the tsetse fly *G. pallidipes* will feed on *Euphorbia Tirucalli* and other latex-bearing plants. As this was opposed to previous observation and to the finding by Lester and Lloyd that the digestive enzymes of tsetse flies are adapted to the digestion of blood but not of plant juices (1928, *Bull. ent. Res.*, **19**: 42), it became advisable to repeat the Natal experiment. Potts and Herbert Lloyd experimented independently, the former on *G. swynnertoni* and *G. pallidipes*, the latter (closely following Mr. Davidson's technique, particulars of which the latter kindly supplied to me) on *G. morsitans*. Neither was able to confirm the claim. Two flies in all in these experiments, both *G. morsitans*, probed the specially-warmed plant—as they will probe any warm surface—but these at once withdrew their proboscides and spent some time in cleaning them. All the remainder refused to probe. All the flies used were hungry and all at once fed on man after refusing the plant persistently. I looked for indirect evidence but was unable to find that tsetses were any more present, or in "feeding-ground" proportions, in localities with much *Euphorbia tirucalli* or *E. matabelense* than in those that lacked them completely. Mr. Davidson's result would appear to have been merely that obtained by Fuller and Mossop when they induced captive tsetses to probe specially-warmed grapes that they had refused to probe when at air temperatures (Fuller & Mossop, 1929). Carpenter (1913 : 30) on the strength of objects found by him in the gut and proboscides of *G. palpalis* concluded that tsetses do sometimes suck water or plant tissues. Otherwise, the tsetse, on the large mass of the evidence available to date, remains purely a blood-predator.

(b) Experiments with water.

As regards the utilisation of water, "preliminary experiments showed that *G. swynnertoni* and *G. pallidipes*, allowed access to water, damp earth (saturated) and 'Manyara' (*Euphorbia Tirucalli*), survived captivity no longer than did flies denied access to any kind of moisture. Flies kept with water available under rat-skin, although they pierced the skin to such an extent that its surface

was covered with drops of water which had oozed through the openings so made, were apparently unable to use the water" (W. H. Potts). Lester and Lloyd found in Nigeria that large feeds of water were fatal (1928 : 58).

(c) Experiments and observations on crocodiles.

Lloyd and Jackson shot three crocodiles (*C. niloticus*) at different times on Riamugasire Island. In two cases the catch of old females was larger at these crocodiles than would have been obtained with man as bait; in the third it was not.

Lloyd next lassoed, bound, and chloroformed a large live crocodile on the island. "The effects of the chloroform wore off after twenty minutes, but as the crocodile kept quite docile no more was given in case it should act as a deterrent to the flies" (*G. palpalis*). The latter were scarce and did not attack any definite part of the body as they had been seen to do on crocodiles basking on semi-submerged rocks in the lake.

A fly catch was carried out over the crocodile, with a simultaneous control catch, concealed from any flies that might visit the crocodile, some twenty-five yards away.

TABLE 39.

Results of simultaneous catches of *G. palpalis* (*a*) at a live crocodile and (*b*) at man.

Catch	Males	Females	Total	Female %	Old ♀♀.	Mean hunger stage
Crocodile .	42	7	49	12	4	3·15
Control . .	28	0	28	0	0	3·16

The site of the catch on the crocodile, however, gave, on the following two days also, more females than did the control site. Moreover, the catch on the crocodile gave no more females than did the two subsequent catches in the same site. It is concluded that catches on crocodiles, live or dead, may fail to raise the female percentage at times when all the hungry females would be showing themselves in any case in the site in which the catch is made. When, on the other hand, there are more females present in an intermediate stage of hunger, it would be expected that the crocodile would raise the percentage of females in the catch. The continued high female percentage after the crocodile abandoned its lying-up site might have been due to the previous formation at the crocodile of a small fly concentration which, as in Nash's observations, continued for a time after the disappearance of its cause.

Experiments were carried out also on the bound crocodile to see from which places the flies could draw blood. This they did from around the eyes, the armpits and the bases of the legs. A dead crocodile, also, was pricked with a pin, when blood flowed from the top of the head, the nostrils, and especially from the fold of skin continuous with, and immediately behind, the mouth. From the back but little blood could be drawn except from the membrane between the "scales" (osteoderms). From this it came freely.

"On the conclusion of the experiment the (live) crocodile was released, and it immediately made for the water. It has not been seen in the same locality since" (Lloyd, report). Evidently, like human beings, crocodiles do not like pin-pricks.

On many occasions it had been observed that dragonflies were circling round a swimming crocodile as much as 30 yards from the shore, the head only of which was visible above the water. It was thought that possibly these dragonflies were hunting tsetse which might be feeding on the crocodile's head. Observations were therefore carried out to discover if tsetse were present, and, if so, to obtain indications on what part of the head they might be feeding.

For this a rock partly concealed by papyrus and overlooking a favourite haunt of crocodiles was chosen. At this spot four or five crocodiles sunned themselves regularly on semi-submerged rocks. It proved possible to see with the aid of a pair of field-glasses that tsetses were present. Even when the whole of the crocodile was out of the water, the flies tended to cluster round the head. None were seen round the armpits or other areas on the trunk where soft patches of skin might be expected. Most of the flies congregated on the flat area just above the eyes. Other places on the head where the flies liked to perch were round the eyes, on the nostril and on the fold of skin continuous with, and immediately behind, the mouth. Flies also investigated the margins of the mouth but did not tend to stay there. The experiments referred to above showed that blood can be drawn from these areas.

When a crocodile is swimming in the water all except the margins of the eyes and the crest of the head are subject to spray which would prevent flies from settling on any but these positions. The flies cluster especially on the crest of the head, even when places that appear more vulnerable are exposed, and doubtless obtain feeds there. When a crocodile swims off a rock with its head above water the flies remain on it. Directly it becomes entirely submerged, they fly off in a cloud to the shore (Herbert Lloyd, report).

(d) Animals used for food.

(i) *Differences in the prey of certain species of tsetse resulting from differences between their areas of search.*

The varying habitat-combinations (vegetational concurrence requirements) of the several species of tsetse have been described already; it will be readily understood that the effect of the very great differences in them will be to bring each species into contact with different combinations of food animals and to cause or accompany differential adaptation of habits in relation to food animals.

G. palpalis, living by water, is far more in contact with crocodiles and monitor lizards (*Varanus niloticus*) than is (for example) *G. morsitans*. It is also, it is true, in contact with situtunga and hippopotamus and will so utilise other game also, when the latter enters its range, that in places it may even appear to prefer it; but its habits are primarily adapted to finding the reptiles referred to. *G. tachinoides* has been shown by Johnson and Lloyd, and Pomeroy and Morris (1932), to be equally independent of game.

G. morsitans and *G. swynnertoni* live in game country and their habits are closely adapted to those of the game animals, though *G. swynnertoni*, using the small thickets more, has perhaps the wider food-range, even though these be its breeding-ground.

G. brevipalpis, spending the day in dense thickets, mainly at their contact with savanna, open spaces, and paths, is more closely in touch with dense-forest animals, such as bush-pig, buffalo, suni (*Nesotragus*), elephant, and baboon; and it attacks in the thickets by day. Guinea-fowls, especially *Guttera* (the crested genus), and the dense-bush francolins (e.g. *Francolinus squamatus*), will be the chief birds that it will meet.

Nevertheless *G. brevipalpis* leaves its thickets after sunset, and our recent observations on Maboko Island confirm old observations by myself (Swynnerton, 1921 : 360) which suggested that it may hunt in the savanna by moonlight. It should then find game animals generally.

G. pallidipes and *G. austeni* very definitely "have it both ways," for hiding, breeding, and attacking in the thickets; they also search freely by day the open savanna wooding which forms the home of *G. morsitans*, and *G. pallidipes* (at least), the yet more open mbugas and glades which serve *G. morsitans* also as feeding-grounds.

The importance of bush-pigs, *Potamochoerus koiropotamus* Desmoulins, as hosts for the three flies *G. austeni*, *G. pallidipes* and *G. brevipalpis* is undoubtedly very great. "Beyond Zigi village—where tsetses (*G. brevipalpis* and *G. austeni*) were most numerous—was the location also of the most extensive feeding-grounds of pig" (Wallace). Numerous observations by myself in various localities bear out this view, while, in my experiments on carnivorous animals, these liked bush-pig better than any other animal offered to them. The bush-pig is, moreover, very difficult to exterminate.

(ii) *Range of size and conspicuousness in the animals attacked.*

The size and conspicuousness of the animals on which tsetses have been seen feeding under natural conditions have varied from those of the rhinoceros to those of sleeping snakes.

(α) *G. palpalis* and *G. tachinoides.*

Simpson observed both *G. palpalis* and *G. tachinoides* feeding on a puff-adder (probably *Bitis gabonica*), and Carpenter has seen *G. palpalis* feeding (one fly in each case) on a python (*P. sebae*) and on a small snake. Lately, on Riamugasire Island, Jackson and myself found a tortoise beset by *G. palpalis*, one of which flies was definitely seen to feed on it. In the next four days Jackson repeated the observation on two quite small tortoises. Fiske records the same thing, stating that a white ring composed of the flies' excreta round the eyes of some of the tortoises showed how much they were fed on. This, with the instances of the snakes, suggests that tsetse flies are capable of finding both small and inconspicuous animals, not necessarily with rapidity of movement. Even *Varanus niloticus*, the common monitor, though huge for a lizard, cannot be regarded as a large animal or one that is conspicuous in its natural surroundings, yet it forms so regular a food for *G. palpalis* that Carpenter, in his examination of the gut contents of that tsetse, found that the blood of *Varanus* figured more frequently therein than that of anything else and noted cases in which these lizards, with only their head showing above water as they swam, were being attacked vigorously.

(β) *G. morsitans.*

There is a great deal of evidence that goes to show that this species feeds mainly on what is loosely called game. It is found, nevertheless, in east Africa in well-fed condition during the rains and early dry season when game is often exceedingly scattered and scarce. It will be seen that we believe this to be the effect of air-moisture entirely, with feeds very many days apart. At the same time there is as yet no proof that this fly fails to detect the smaller or less conspicuous objects that attract *G. palpalis*, and its possible use of other hosts still demands further work.

Thus gut-examination has not (so far as is known) been carried out exten-

sively in any of the numerous areas in Africa that swarm with francolin and guinea-fowl, or the more limited areas in which cane-rats (*Thryonomys*) abound, so that it is impossible to guess the extent to which *G. morsitans* might in such parts, even in small numbers, tide over the two starvation months of the year with their help. Johnson and Lloyd, with W. A. Young and H. Morrison, examining the food of *G. morsitans* in Nigeria by means of the precipitin test, found the blood of small antelopes to preponderate in most cases with a proportion of avian blood in only 0·05% of the flies examined; but they found avian blood in 17% of the flies (*G. morsitans*) in one month at one focus, large game being scarce (1924, *Bull. ent. Res.*, **15**: 26). " In the case of vultures, tsetses (*G. pallidipes*) have been noted hovering about the region of the head on two occasions " (Curson, 1924). In a series of captured *G. morsitans* examined by Llewellyn Lloyd in Northern Rhodesia, he found that of the specimens in which the blood content could be identified 15% contained non-mammalian blood.

It should be noted that the precipitin test and normal observation generally can as a rule only tell us what the flies are feeding on. It is only when the " easier " species of prey are removed that this test will tell us what the flies will feed on. More is said on this subject on p. 284 below.

(iii) *Range of food animals as affected by the preferences of the tsetses and by the animals' wholesomeness as food.*

(α) *Introductory.*

In a series of experiments that I carried out, I found that all the carnivorous vertebrates tested possessed very strong preferences in the matter of food. Only hunger would induce them to take certain species of prey, and between these and the species that space would be found for, even under conditions of repletion, there was a fine gradation corresponding with degree of repletion. The ill-effects on the predators of some of the mistakes that were made showed that these preferences were not merely a matter of whim, taste, or scent, but that actual nauseousness, and therefore probably unwholesomeness, was the cause of the rejections. The same meats cooked were eaten readily and without bad result by the animals which rejected them raw. In one or two experiments bloods were tested with similar result. Three species of carnivorous insects were tried in the rôle of predator—a dragonfly (*Anax dorsalis*), a robber-fly (*Alcimus rubiginosus*), and a driver ant (*Dorylus nigricans* var. *molestus*); all showed unexpectedly strong preferences (Swynnerton, 1916).

It does not follow from the above that tsetse flies would also show preferences or that they might thrive differentially on different kinds of (say) mammalian blood, but it does follow from the conclusion that the flesh of different species differs apparently in its properties, and that experimentation on the tsetses in this connection would be worth while. A series of experiments, to be carried out by the entomologist at Shinyanga, has been based on this view; but it has as yet been barely begun.

(β) *The preferences so far noted on the part of the tsetses.*

G. morsitans, *G. swynnertoni*, and especially *G. pallidipes*, *G. brevipalpis* and *G. austeni* attack cattle far more readily than they attack man. A little of the evidence for this has been given on p. 34 above, and it has lately been confirmed experimentally for *G. morsitans* by Nash. In my experiments, *G. morsitans* and *G. pallidipes* attacked man more readily than goats and preferred ox to goats and sheep. An individual of *G. pallidipes* that was seen

to allow native carriers to pass it unmolested at once attacked a donkey (stallion) when this arrived. In an experiment with some *G. pallidipes* and many *G. brevipalpis* enclosed in a large, furnished net " a live goat tied inside the net attracted little attention. The flies bit occasionally, but allowed themselves to be driven off easily, and none fed to anything like repletion, yet the two oxen, when brought close up to windward, always attracted a great rush, even on the part of females that had been resting quietly on protective bark surfaces and had not been in the least attracted by the goat. I should say that I was myself much more readily attacked in the net than the goat " (Swynnerton, 1921 : 368). Moreover, Jackson and I obtained some evidence of a strong preference on the part of *G. palpalis* for tortoise as against man. Flies in the presence of abundance of food animals (game in the case of *G. morsitans*, reptiles in that of *G. palpalis*) show themselves in small numbers to man, but those that are hungry still feed on him. Carpenter (1919 and 1924 : 190) deduced from the examination of the corpuscles contained in large numbers of *G. palpalis* that reptiles were much preferred to mammals and situtunga antelope to hippopotamus. The relative reluctance shown by Dr. J. W. S. Macfie's flies to feed on guinea-pigs, dogs and cats is worth recalling, also Buxton and Lewis's loss of flies (*G. submorsitans* and *G. tachinoides*) when fed on guinea-pigs instead of on man (1934 : 178), the preference of Llewellyn Lloyd's flies for monkeys as against goats, and Curson's observations on the preference of *pallidipes* for horses as against cattle (Curson, 1924). Potts's results from guinea-pigs may to some extent be contrasted with those referred to above. The explanation of the difference may be that flies accustomed to feeding on a particular animal may not readily take suddenly to another.

It is worth mentioning here that preferences for individuals of a particular species and of a particular sex have been noted in the past: for individual oxen as against other oxen even of the same colour (Swynnerton); and Moggridge gives the following figures for three bait-oxen, driven about together during a recent series of experiments :—

White ox	attracted	68	flies.
Black ox	,,	54	,,
Red ox	,,	6	,,

A preference for the colour white would be contrary to all previous experience, and it seems more likely that the preference was based on an individual difference in scent rather than on attraction to colour.

Jackson also found one of two oxen preferred by females of *G. morsitans*, though males showed no preference.

The tsetses that come into our clerks' office from time to time have, out of three individuals, bitten one man (Jamenis) on 15 out of 16 occasions; and this has not been a matter of differential colour of clothes. Such predilections are known on the part of other insects as well, such as fleas and harvest mites (*Trombicula*). Fiske found that different fly boys tended to catch female tsetses in different proportions.

Different species of tsetse have different preferences. Thus *G. morsitans* attacks man (an animal suggested by my experiments to be distasteful to vertebrate carnivora) considerably more readily than does *G. pallidipes*, and the latter considerably more readily than does *G. brevipalpis*; while *G. austeni* practically never attacks man at all. *G. palpalis* probably attacks man a little less readily than does *G. morsitans*, for, unlike this species, it does not form " following swarms " on man. *G. swynnertoni* does so more readily.

(iv) *Differences noted in the effect of food on the viability and breeding of the tsetses.*

Potts has found that goat's blood is less suitable for the breeding of the flies than ox blood, and Llewellyn Lloyd's experiments on this subject in Northern Rhodesia, with his conclusion that on a reptile diet *G. morsitans* does not breed well, will be remembered. Potts found human blood (male) at least as good as sheep's. Numerous flies (*G. morsitans*) fed by Potts on a female cheetah in adult coat have in nearly every case taken a first feed but in all cases have refused subsequent feeds and have eventually died without feeding, though ready to feed on man (males only).

Young cheetahs possess the anti-counter-shaded colouring of the skunk and honey-badger, indicative of intensely nauseous qualities and " warning " in its effect. It is lost in the adult in favour of an anticryptic (concealing) coloration that helps the cheetah to hunt, but it is perhaps truly indicative of the status of the cheetah as food. In that case it may have been evolved as a protection against lion, leopard and hunting-dog.

In curious contrast to the above, hunting-dogs (*Lycaon pictus*) have a strong and (to man) most objectionable smell. Yet flies applied by Herbert Lloyd to our tame *Lycaon* bitch have fed and re-fed and thrived—a most unexpected result.

(v) *Animals protected otherwise than by nauseousness,* e.g. *by intolerance, nature of covering, or colour.*

Monkeys (*Cercopithecus*) appear to be in the " intolerant " category, baboons (which cannot be infected artificially) probably a little less so : yet, since both these animals search for food on the ground amongst the flies, it would be strange if they were not sometimes bitten, whatever their intolerance and quickness. It is believed that baboons are much attacked, whether fed on successfully or not. J. J. Simpson records an enormous number of *G. morsitans submorsitans* following a troop of baboons in the Gambia, and notes that the Mandingo name for tsetse means the " biting fly of the monkey " (1911, *Bull. ent. Res.*, **2** : 223). I have myself more than once found *G. morsitans* in some numbers on baboons that I have shot and have been told by natives of numbers of tsetses accompanying baboons raiding their gardens. The susceptibility of monkeys (on the other hand) to experimental infection by trypanosomes suggests that *Cercopithecus* is not fed on in nature to any great extent. R. H. T. P. Harris found in Zululand that a zebra filly was little attacked by *G. pallidipes*. Tested against a dummy of sacking, it was far less attractive than the latter, yet an ox tried against dummies excelled them in attractiveness. Harris put the zebra result down to its colouring, but a fuller control experiment (*e.g.* with the white stripes blacked) would have been necessary to prove this; it may have been due to the striped colouring disguising the form of the animal, or to a negative chemotropism for zebra. It is interesting that Harrison has failed to detect tsetses on zebras with powerful glasses at quite close ranges, though he has watched them freely on giraffes. This may mean nothing, as flies have been found on shot zebras, and giraffes might also have been regarded as protected by broken colouring.

(vi) *Summary.*

My experiments on carnivorous mammals, including lions, showed the following order in their preferences :—" (1) Pig, wild [*Potamochoerus koïropotamus* ♂] and domestic (♂); (2) beef (♂), nearly equal to pig; bushbuck

[*Tragelaphus scriptus* ♂] and sable antelope [*Hippotragus niger* ♂], liked very nearly as much; (3) goat and sheep [wethers], dog, man [♀], and blue duiker [*Philantomba monticola* ssp. ♂]. These last were liked far less than (2)" (Swynnerton, 1921), though a leopard (*Felis pardus*), had it been tried, might have placed dog " higher." In other comparative experiments hare (*Lepus* sp.) and ox were greatly preferred to man (♂). Man was always completely refused, but would doubtless have been eaten under the stimulus of really sharp hunger.

Preference of this kind in the tsetse as between species of wild game may prove of great importance, and it is possible that investigation might even show that certain species of animals could be excluded from game-destruction schemes, should such in the end be necessary anywhere. A number of preferences on the part of tsetse flies have been observed already, both as between species of animals and individuals of one species, and some animals appear to be definitely less suitable than others as food for the tsetses.

3.—THE SENSES BY WHICH THE TSETSES FIND THEIR FOOD.

(a) The sight of the tsetses as deduced from the structure of their eyes.

I asked Dr. H. Eltringham, F.R.S., if he would examine the eyes of some tsetse flies and let me have his views on their capacity for seeing objects at a distance. Jackson collected and sent the flies, which belonged to the three species *G. palpalis*, *G. swynnertoni*, and *G. pallidipes*. The following is an extract from the provisional reply received from Dr. Eltringham, who is now investigating the subject more fully*:—

" So far as we know the eyes of all Diptera are pseudocone eyes, and I find that of the tsetse fly no exception. The theory of vision with a pseudocone eye, and no one has upset it so far, is that the pseudocone, a more or less fluid structure, lying beneath the corneal lens, merely concentrates the light transmitted by the lens, and having little refractive power, is incapable of forming any actual image. The nervous elements therefore receive a number of dots of light of varying intensity, and these form an erect image, just as a newspaper illustration makes a picture out of large and small dots. If the facets are very numerous this image may be quite a good one, as instanced in the comparatively keen sight of the larger dragonflies, which, in spite of statements to the contrary in most of the text-books, have pseudocone eyes. Now the eye of the tsetse is large in comparison with the size of the insect but not more so than the eyes of many Diptera which seem to depend less on sight than does the tsetse.

" I have sections of other Dipterous eyes and I can find only one feature that distinguishes the structure of the eye in tsetse, and that is the shape of the distal part of the visual cells. In other Dipterous eyes the pseudocone is very pointed at its apex. . . . In tsetse the pseudocone is of a somewhat different shape, being broader, and the visual cells into which it fits seem to be expanded to a cup-like shape. This would afford a larger end-area for these cells, and more light would reach them. Unfortunately this does not account for superior sight, as the actual acuity of vision depends rather on the number of light spots and their fineness, just as a newspaper illustration is better the finer the screen through which it was made. On the other hand, the arrangement in tsetse would seem to help the appreciation of movement, as distinguished from form, on the same principle that the facets of the dragonfly's eye are larger above, whence his enemies come, and smaller below for the selection of his prey.

* Dr. Eltringham's paper has now been published (1936, *Trans. R. ent. Soc. Lond.*, **85** : 281–288).

"I understand that tsetse flies are quick to detect movement which if true would support the above suggestion. . . . I think one may suppose that on the one hand the tsetse is well adapted to the visual detection of movement, and that on the other, the explanation of its behaviour is partly psychological, and that its habits have developed in it a greater tendency to use its eyes than is found in, say, the blow-fly, which works so largely by scent."

(b) Sight versus scent: Nash's experiment at Kikore.

Nash carried out in 1929 a well-planned experiment to test the relative importance of the eyes and scent-organs of *G. morsitans*. 750 flies had their eyes painted, 750 their antennae, 750 both, and 750 (the control) neither. All were liberated at one spot and only recaptures outside the radius of a mile from the spot were considered for the purpose of the experiment. Counting only the recaptured flies which had not succeeded in freeing their organs of paint, the numbers retaken were—blinded flies 0, scentless flies 66, control flies 70.

In a laboratory experiment Nash found that the blinded flies in tubes with gauze ends fed as willingly and approximately as often as the controls, while the flies with occluded antennae might be placed in their tubes on an animal but did not feed, the necessary olfactory stimulus failing to reach them. Of the latter flies, only 3% were alive at the end of a month and of the blinded flies 50%.

Nash considered that this indicated that:—

"*G. morsitans* hunts its food entirely by eyesight; the olfactory organs of the antennae are only operative over a very limited field. Possibly they stimulate the fly to probe, and are capable of selecting the best places for the insertion of the proboscis."

He suggested that "the normal action of obtaining food consists of a visual and an olfactory tropism. The stimulus of seeing a moving object induces the reflex of following that object; the stimulus of smelling the object induces the reflex of probing. Should the fly be unable to see the object, it cannot follow it. Should the fly be unable to smell the object, it will be unwilling to probe. Should the fly be exceedingly hungry, a new stimulus is brought into play, which induces probing. This stimulus is sufficiently powerful to be able to induce probing when the olfactory organs are rendered functionless."

(c) Scent experiments with tsetse traps.

Since Nash's experiment was conducted a number of experiments have been carried out on *G. pallidipes*, *G. swynnertoni*, and *G. palpalis*, in which scent bait (a bull calf; later gland extracts) was placed in traps and in which the resultant catch was commonly from two to three times as high as the usual catch without scent or as that of the control. It might very well have been that this was still only a close-range effect; that the flies were all attracted by sight, but, perceiving the scent on arrival, made more desperate attempts to reach its source, so that more entered the traps. For *G. swynnertoni*, caught in smaller numbers, this could easily have been the explanation, and it is indeed supported by an experiment by Lloyd on *G. swynnertoni*. But in the case of *G. pallidipes* it was probably not; for it was by no means my impression, from sitting and watching traps in the best hours for catching in the late dry season in Shinyanga, that many females that visited traps which did not contain animal bait left them without being caught. The catch of the females of this fly that came to the traps was nearly 100% effective; such individuals of *G. pallidipes* as sat about on the outside of a trap and did not get caught

were males. It is therefore relevant to the argument to observe that, in a series of experiments in which an invisible bull calf was used as the bait and in which great numbers of flies were taken, the male percentage hardly altered. The female percentage was 75·02%, while that of the control was 77·88%, or only 2·86% more. Moggridge found later that an SY trap, normally nearly useless for *G. pallidipes*, caught that fly in large numbers when cattle were ploughing to windward of it, but not at other times; just as the SS (AS) trap, normally poor for *G. swynnertoni*, captured this fly also under the same conditions—but not at other times. The traps were from 10 to 20 yards from riverine thicket containing *G. pallidipes*, and in the bay of a bend in the stream. The team of six oxen was to windward in open country and ploughed nearer and nearer. Watching the traps with the team passing and repassing them Moggridge saw no flies at them till the distance had been reduced to (say) 50 yards from the traps. Then flies began to appear at the traps and a large catch accumulated in a very short time. Under these conditions one of the traps (SY 3), which normally caught hardly any flies, caught 139, 58, and 107 flies on 29th, 30th, and 31st October. Whether the flies were attracted to these traps by a scent appreciated at a distance or whether the increased catch was due to more effort on arrival as the result of the scent that was reaching them, it seems likely that the increased catch was due to distant appreciation of scent. Sight attraction to the cattle should have taken the flies to the animals; the traps had been in view at close range from the flies' headquarters all the time.

In the experiments on *G. palpalis* by C. B. Symes gland extracts were used, not live animals. The results (as regards increase of catch) were the same.

(d) Previous scent experiments.

In an experiment of mine in which large numbers of *G. brevipalpis* and some *G. pallidipes* were confined in a large mosquito net and cattle driven past to windward, strong reaction (in the shape of a general flight to the windward side of the net) took place on the part of the flies even when a screen of shrubs made it impossible for the cattle to be seen through the net. Such reaction did not take place in the control experiments (*i.e.* those on the leeward side of the net) unless the cattle were brought quite close up to it (Swynnerton, 1921 : 367).

Fuller and Mossop (1929 : 11–14) surrounded a cow and a calf with a hessian screen in a thicket and found that the flies came to the screen in nearly as great numbers (0·8–0·9 per minute) as when the animals had been unscreened in the thicket (0·8–1·4), but did not come to the screen when animals were absent. Under the latter conditions on several visits by the observers only one fly in all was seen on the screen.

Lamborn (1915) records : "I have found repeatedly that if well starved flies with one wing clipped are released in long grass, they will make their way by running to a person sitting at a distance of ten to twelve feet, whom it is impossible for them to have seen. The sense of smell, therefore, must play an important part in leading them to their prey." The proportion recovered is unfortunately not stated, for this would have shown how many flies went in other directions.

(e) Provisional conclusion.

It seems possible, despite Nash's excellent experiments, (i) that scent in the air can be appreciated by tsetse and may lead them to probe where they sit (as I have myself seen in some of my experiments on flies in large mosquito-

nets), or to fly to conspicuous objects within sight at the time; (ii) that it is not a sense of precision, while sight certainly is, *Glossina* being able to fly to any conspicuous object; and (iii) that when sight has brought the fly to an animal, close-range scent will tell the tsetse, if sight has not done so already, that this is an animal of a species that it is hungry enough to feed on and will act as a stimulus to probing. The fact that no blinded flies were recaptured by Nash except those that had cleaned their eyes counts really for nothing, for anyone having seen tsetse with their eyes painted would realise that, unless they clean them, they are finished. They dash into the nearest object, or tower like rocketing pheasants. A blinded lion would be equally powerless to reach its prey, despite its magnificent scent. That the recaptures of the flies with varnished antennae and the flies of the control should in Nash's experiment have been nearly equal, is at first sight striking and is the point in the experiment that tells against the usefulness of scent. But on the lines of his own explanation and laboratory experiments, the scentless flies should have been generally hungry to the point of starvation as a result of the lack of the stimulus to probe and the failure therefore to feed on previous encounters with prey. Therefore, continuing hungry, they would have been coming to all animals and men that they saw—far more eagerly than the control flies, which would have had previous meals. This might have made a much greater difference than the 23% Nash allowed. On the other hand, he considers that intensity of hunger may replace actual scent as an incentive to probe.

It may, of course, be that some species, perhaps those that use thicket most freely—*G. pallidipes*, *G. austeni*, *G. brevipalpis*, and *G. palpalis*—make more use of scent than do *G. morsitans* and *G. swynnertoni*. Adapting Dr. Eltringham's suggestion, it may be that the habits of these last two flies in places (or generally) have " developed in them a greater tendency to use their eyes," to the detriment of their use of their scent-organs. An experiment of Lloyd's at Shinyanga, in which flies (*G. swynnertoni*) released from boxes went under equal conditions in as large numbers to a control target as to one containing a calf, favours those who consider that sight is the factor and not scent.

More experiments are wanted on each of the species of tsetse.

4.—THE VISUAL PERCEPTION OF MOVEMENT AS AN AID TO THE FINDING OF PREY.

(a) Conclusion based on general field observation.

It has been observed universally that tsetses of both sexes are attracted in great numbers to the chase of fast-moving objects, which they overhaul and which, if inedible, they ride on or in for great distances. The eyes of insects generally are adapted to the perception of movement, though the movement will usually be that of an enemy at close range that has to be dodged, or fairly close-range prey, or individuals of the other sex, which, however, are not recognised visually till they are nearly reached. The tsetse is probably pre-eminent amongst insects in respect of the distance from which it proceeds to the attack.

(b) Distance of attack.

Our recent experiments dealing with this are given on pp. 303 and 304 below.

5.—THE MEANS BY WHICH THE TSETSES PRESERVE CONTACT WITH THEIR FOOD ANIMALS.

(a) A fallacy corrected as to the continuous association of tsetses with game herds.

Tsetses, especially males, but females also, will ride on man and animals for a time. A fallacious idea has arisen from this that a fly community will follow

a game-herd continuously and so appear wherever the game-herd does—far outside of the normal fly limits. Actually the flies do not live in continual association with their animal hosts. "They feed on the animals when they find them, and immediately afterwards fly off to digest their meal. Thus individual tsetses do not continue to follow any particular herd of animals through the bush, but set forth afresh to seek for food as they become hungry" (Jackson). As the need for a feed will not recur for from two to four days in the dry season and for eleven or more in the wet season, it will be seen that there is plenty of time for the flies to lose contact with a herd.

(b) The contingencies which have normally to be met by the game-feeding tsetses.

Game may be scarce, yet regular in its habits and may never completely desert a locality. On the other hand, most or all of the animals present may desert a sub-locality in which (for example) water has dried, or the grass is old, for one in which water survives or young grass has sprung up following burning; they will form regular habits in the new centre.

These two contingencies characterise, or alternate in, the bulk of the country infested by *G. morsitans* and *G. swynnertoni*. The problem before the fly is (*a*) to establish continually-repeated contact with the game that is present, and (*b*) to find the game when it moves off to new water-holes and new grazing. Where enormous influxes of game take place annually from outside the fly belt, as happened in south-east Kikore, the position is not really altered. The fly has an extra food supply while it lasts and keeps in touch with it by the ordinary means. Being unable to follow the animals out again through unsuitable country or distances, it has to fall back, when they go, on the small permanent game population.

(c) The feeding-ground habit.

The regularity of the habits of ungulates when undisturbed, their use of paths, and their tendency to utilise as grazing-grounds or passages glades and mbugas, the openness of the larger of which also gives them protection from lions, have enabled the flies to adopt habits which keep them in regular contact with the resident game. They use these paths and these openings as feeding-grounds which they visit and search when hungry.

(d) Re-discovering game that has moved.

While the fly does not follow the game individually very far, a definite game concentration may indirectly draw in the flies from the surrounding bush and so cause a strong local fly concentration. Nash determined part of the mechanism by which this came about. The flies, he found, follow game-paths, and in this way a large game concentration is liable to be succeeded by a fly concentration at the spot to which the paths converge. Part of his area at Kikore was subject to immigration on the part of large numbers of game which came in from the Masai Steppe and concentrated about water-holes. When these were dry, the game departed. He showed, from the game-fly concentrations which he studied, that there was a lag on the part of the fly numbers both at the beginning and the end: the game concentration preceded the strong fly concentration and the latter continued for some weeks after the game had dispersed, while tsetses marked and liberated over a mile away in the general woodland were still for a time attracted to the now dry water-holes. This supported the conception that it was the paths rather than the animals themselves which guided the tsetses to the concentration site.

He was able, further, to form a fly concentration where no concentration at

that time existed either of game or of fly by making six paths that converged to one of two pools. A concentration of the flies formed here. No concentration formed at the second pool to which no paths were made, though this pool becomes equally the site of a fly concentration when game concentration takes place. When the grass grew over the paths the concentration dwindled; when they were cleared again, it was renewed. Throughout the course of the experiment 678 flies were marked at the pools and only 17 were recaptured there, so that clearly the concentration was composed of ever-changing individuals, as previous work also had indicated. It was not a strong concentration as compared with a natural one. Nash suggests as a reason for its relative weakness the lack of " the very strong animal smell that exists round the water when game are present in large numbers." As the experiment took place at the time of the year when the hunger-cycle is longest, it may also have been lack of hunger which prevented full concentration.

Fiske ascertained that *G. palpalis* followed game trails and human pathways. C. W. Chorley has lately been able to confirm this. H. Harrison is finding in Block 9 at Shinyanga that a general movement of game to a new part of the block is followed gradually by a transference thither of the heavier infestation of fly. This may be because flies wander about looking for game, and feed and drop off when they find them. It follows that where the game are more numerous, more flies will drop off, and the neighbouring rest-haunts will contain more fly.

6.—THE GENERAL RELATION OF THE TSETSES TO THE DIURNAL VERTEBRATES.

(a) The diurnal vertebrates with which the different tsetses can make regular contact during their season of stress.

(i) *The lake-shore reptiles and the wild ungulates.*

The crocodiles (*Crocodilus niloticus*, also, in Lake Tanganyika, *C. cataphractus*), monitor lizards (*Varanus niloticus*), and tortoises of the lake shores, for *G. palpalis*, and the ungulates for this and the other tsetses, are obvious and favoured foods; they fulfil in many places in every fly belt the condition referred to above, and no more need be said of them at the moment. The remaining main groups are as follows :—

(ii) *The carnivora.*

Lions, though mainly nocturnal, hunt also by daylight when undisturbed, despite much that has been written to the contrary, and move and show themselves openly by daylight in any case. Hunting-dogs (*Lycaon pictus*) hunt much by daylight. Cheetah appears to be unacceptable to some tsetses at any rate. The numbers in which these animals can occur, and their availability therefore to the flies, are limited by the numbers of the ungulate population, so that in the event of the destruction of the latter the carnivores would not long be available. Mongoose parties (in particular, parties of the Banded Mongoose, *Mungos mungo*) are fairly common, but these animals are very quick and probably quite intolerant, even if they are acceptable.

(iii) *The domestic ungulates.*

Cattle in the Tanganyika Territory, in the late dry season especially, when the fly most needs this extra supply, are often herded by their native owners for some miles into the fly belts, the risk of loss from tsetse being regarded as a

more remote danger than the certainty of immediate wholesale destruction by absence of grazing elsewhere. They are freely attacked and are probably a valuable adjunct to the fly's normal foods. It has been found by Ruttledge that in the Koalib hills in southern Kordofan *G. morsitans*, with game exterminated except for a very few individuals, is living successfully on man, his cattle, and especially his pigs, the animals having acquired great tolerance or immunity to the local trypanosome strains though they die when subjected to others. I refer later (on p. 295 below) to the fact that an increased and flourishing fly population followed the premature introduction of great numbers of cattle in one of our experimental blocks. The rôle of the native's cattle in helping to spread the flies is discussed on p. 298 below.

(iv) *The primates, insectivores, and bats.*

Dr. W. B. Johnson and Dr. P. H. Rawson, in Nigeria, using the precipitin test, found in one case that of 42 individuals of *G. morsitans* 9 gave positive reaction to man, 8 to baboon. Man is continually in the fly haunts in numbers, variously occupied. He lives in fly country and forms roads and paths which the flies then use as feeding-grounds.

Though man is regarded as an " intolerant " animal, natives in our experience rarely kill a tsetse, and many a tsetse successfully extracts and flies away with a full feed from a man. At the same time man is hardly, with any species but *G. tachinoides*, a " preferred " food animal, and it is unlikely that he could by himself long support a tsetse community. Baboons, it is believed, are attractive to the flies, Vervet monkeys (*Cercopithecus aethiops*) perhaps not. Jack (1934) writes of his attack on the game that the fly (*G. morsitans*) disappeared with the reduction of the latter in spite of the continued presence of numerous baboons. " It appears very probable that too great a proportion of the flies attempting to feed get caught and killed by baboons for these animals to constitute an economic staple diet for the flies. . . . In these circumstances baboons may be allies rather than otherwise. The more the game is thinned out, the more hungry flies are likely to attack the baboons, and the more they are liable to get caught and killed " (p. 29). This is probably the first time in history that the baboon has been accorded a halo !

The presence in some intensity of man's activities does seem inimical to *G. morsitans*, despite the fact that it feeds on man. It is not so to *G. swynnertoni* or to *G. palpalis*.

The Insectivora—hedgehogs and shrews—are much more likely to dispose of a tsetse than to be bitten by it. Of the usefulness or otherwise of bats nothing is known, but they will be found only by resting flies which chance to utilise the hollow trunks which the bats also use—and resting flies are commonly moderately replete. Fruit bats (*Epomophorus* and *Rousellus*) often hang up many together in the daytime in quite low foliage in fly country.

(v) *The rodents.*

The larger species—the porcupines (*Hystrix*) and spring-hares (*Pedetes*)—are nocturnal and lie up in burrows in the daytime. The true hares (*Lepus*) are less seen in daytime than at night, but are doubtless sometimes found in their forms. They are seldom really abundant, they do not specially frequent the feeding-grounds of the flies—in fact, the reverse—and the flies cannot therefore count on finding them at particular spots. Much the same applies to the species of field-rats, some of which move freely in the daytime. Every few years the density of certain species of these becomes enormous, one sees

them running about everywhere even in the heat of the day in numbers that are amazing, and amongst other activities they inflict immense damage on cotton. It is unlikely that during this peak of the cycle of the rats the tsetse flies would not try to feed on them; but it is likely also from tests on rats in captivity, that the tsetses would seldom succeed. Then the rats drop rapidly in numbers and are hardly seen for some years, so that, if they ever were a source of food, they are not a dependable one. Nor in their years of scarcity do these species specially collect in spots which might be used by the flies as feeding-grounds. Moreover they do not, in fact, appear often to be bitten in nature, for they are susceptible to artificial infection by trypanosomes. Other species, it is true, live in the feeding-grounds, for particulars of which see appendix 5.

The cane-rats (*Thryonomys*) are large enough, and permanent enough, to be attractive. Though plentiful locally, they are usually localised, and large tracts of country are without them. It is not known whether the loose grass-covering with which they roof their haunts would suffice to prevent their detection by the flies.

(vi) *The birds.*

Tsetses creep under the wing of a bird to feed or attack it on its bare parts, but they do not hunt apparently above ten feet from the ground, nor is it likely that a small bird will permit itself to be fed upon. The following are thus left:—

(α) STRUTHIONIDAE (Ostriches).

While inhabiting mainly open plains (pl. 2 and pl. 11, fig. 1), the ostrich (*Struthio camelus massaicus*) enters the thorn-bush which intersperses or borders them and the feeding flies enter the plain margins. It is probably fed on considerably.

(β) LIMICOLIDAE (Plovers, Stilts, Snipe, Sandpipers, Coursers, and Stone-Curlews), OTIDIDAE (Bustards), and GRUIDAE (Cranes).

Of the Greater Bustard the same may be said as of the Ostrich, though it tends to keep more strictly to the open. The Lesser Bustards, Floricans, or Knorhaans (*Lissotis*, *Ophotis*, and *Lophotis*), are relatively common in tsetse bush, that of *G. swynnertoni* particularly, and their tendency to haunt the concurrence of bush and open would bring them in contact with the feeding flies. The same would apply to the coursers (*Cursorius* and *Rhinoptilus*) and spur-winged and wattled plovers (*Hoplopterus*, *Stephanibyx*, *Afribyx*)—all probably too small to be tolerant—and the Stone Curlew and Water Dikkop (*Burhinus capensis* and *B. vermiculatus*). In the RECURVIROSTRIDAE, Snipe (*Capella media*, the Double Snipe, and *C. nigripennis*, the Ethiopian Snipe) are in swampy locations (as near Tabora) enormously abundant in the rains. The Painted Snipe (*Rostratula benghalensis*), in less numbers together, is widely distributed at all times. The Wood and Common Sandpipers occur at the smallest waters. Cranes, too, particularly the Crowned Crane (*Balearica regulorum*) which is very common, like open or swampy spots, but all the birds cited above, though found most in the open, are commonly available at the contacts and even in the wooding itself.

(γ) PELECANIDAE (Pelicans) and PHALACROCORACIIDAE (Cormorants and Darters).

The Cormorants (*Phalacrocorax africanus* and *P. lucidus*, less numerous inland), Darters (*Anhinga rufa*) and (with them) Egrets (*Bubulcus ibis* especially)

form populous colonies in groves of tall ambatch bushes projecting above the marginal waters of the lakes. These are exactly in the line of search of *G. palpalis*, but, from the fact that Carpenter, out of 46 flies of this species examined, found avian blood in two only, or 4·3%, it would seem that, while it can use birds, at that time and place it utilised them but little. Whether, with crocodiles and Monitor Lizards (*Varanus niloticus*) greatly reduced, the fly would use birds more cannot be known without the experiment in reduction. Corpuscle measurement and the precipitin test can tell us nothing except in conjunction with the latter.

Cormorants and (often) Darters occur also in numerous waters throughout the ranges of the woodland tsetse. Pelicans occur in the larger waters and visit some of the smaller.

(δ) ARDEIDAE (Herons, Egrets, Bitterns), ANATIDAE (Ducks and Geese), and RALLIDAE (Rails, Moorhens, Gallinules, and Jacanas).

The Herons—the ordinary Grey Heron, *Ardea cinerea*, and the Goliath Heron (*A. goliath*), the Purple Heron (*Pyrrherodia purpurea*) and other herons, egrets, and bitterns—use streams, swamps, and isolated pools in our fly belts generally, and, if tolerant enough, are readily available to the tsetses. Usually, however, their density is definitely low. Cattle Egrets (*Bubulcus ibis*), in flocks, follow cattle and game for the grasshoppers flushed by these animals. They also frequent open patches.

Of the Ducks, again, it can be said that they haunt waters, whether streams or vlei-pools, that lie within the tsetse fly feeding-grounds. They may be in very great numbers but their haunts tend to be widely separated in the dry season. In the rains they may be found everywhere. Moorhens and Coots (*Gallinula* and *Fulica*) swim in, and Jacanas (*Actophilornis* and *Microparra*) run over the waterlily leaves of, nearly every piece of long-lasting water. The Black Crake (*Limnocorax flavirostra*) is similarly distributed.

An impediment in relation to birds attracted by water is that the survivals of that element in open form become very widely separated in the late dry season.

(ε) SCOPIDAE (Hammerheads), PLEGAIDIDAE (Ibises and Hadadas), CICONIIDAE (Storks), and PHOENICOPTERIDAE (Flamingoes).

The most generally abundant of the storks is the "Rain-bird," *Sphenorhynchus abdimii*. This mostly haunts settled country that is completely open (pl. 18, fig. 2), but it follows locust hoppers into the open spaces of the fly bush (pl. 15, fig. 2, whole foreground) and is found there on other errands. The Sacred Ibis (*Threskiornis aethiopicus*) has much the same ground habits as the Rain-stork and these two are often accompanied by flocks of Egrets (*B. ibis* and *Egretta garzetta*). The Glossy Ibis (*Plegadis falcinellus*) and the Hadada (*Hagedashia hagedash erlangeri*) haunt water margins. The White Stork (*Ciconia ciconia*) is sometimes locally very abundant, and in fly bush (*e.g.* pl. 1), but seldom stays long. The Open-Bill Stork (*Anastomus lamelligerus*) resembles the herons in its feeding-grounds. The Marabout (*Leptoptilos crumeniferus*) may be found in most of the situations referred to, but, generally speaking, is not sufficiently common in a given locality to be of much use and is attracted to any place in which there is carrion. The Saddle-Bill, Woolly-Neck and Wood Ibis are less often seen. The Flamingoes (*Phoenicopterus ruber* and *Phoeniconaias minor*) line the edges of the smaller lakes in vast numbers. *Scopus umbretta bannermani*, the Tegwan or Greater Hammerhead, especially frequents glades,

such as form tsetse feeding-grounds (*e.g.* pl. 3), where any small water, temporary or permanent, is present, and must be in constant contact with the flies.

(ζ) COLUMBIDAE (Doves) and PHASIANIDAE (Guinea-fowls—Horned, Crested and Vulturine, " Spur-fowls "—*Pternistis*—other Francolins of many species, and Quails).

The Turtle-Doves (*Streptopelia*) Metallic-Spotted Doves (*Turtur*) and Long-tailed Dove (*Oena*) and the Gallinaceous birds mentioned frequent roads and the contacts of bush and open—the very spots tsetse flies feed in; and they visit waters in numbers together. They are often extremely abundant and the Guinea-Fowls and Francolins tend to be so in particular by the riverside and in other coverts (pl. 3, fig. 2 and pl. 4) that so often intersperse the seasonal concentration grounds of the tsetse.

Sand-grouse of the family PTEROCLIDIDAE (genus *Eremialector*), flighting to waters and found often in tsetse contacts, may be included here. They and the Quails are perhaps hardly likely subjects.

(η) SAGITTARIIDAE (Secretary Birds), AEGYPIIDAE (Vultures), and FALCONIDAE (Hawks, Eagles, and Falcons).

Tsetses have been watched at vultures by Curson. Vultures are in great numbers and are frequently on the ground, but they would in any case disappear if the game were to do so. Of the rest, the Secretary Bird (*Sagittarius serpentarius*) is the most likely to be attacked by tsetses. It uses open plains, but is often within reach of the tsetse flies and is found in fly cover also.

(θ) CORVIDAE (Crows), CUCULIDAE (Cuckoos), BUCEROTIDAE (Hornbills), and CAPRIMULGIDAE (Nightjars).

The species of these families rest or work on the ground. The Ground-cuckoos (*Centropus* of several species) and the Ground Hornbill (*Bucorax*) are the chief possibilities. Tsetse flies (*G. morsitans*) have definitely been noted (by Llewellyn Lloyd) feeding on the bare head-parts of the Ground Hornbill—which, in small parties, searches the ground in all types of country for food. The Nightjars with their highly procryptic coloration can probably be ruled out, though it is true that they commonly rest in the daytime in the actual breeding thickets of the tsetses. The Lark-heeled Ground-cuckoos, frequenting grass jungle and the edges of long-grassed vleis, might possibly be attacked, especially when they bask, as they do habitually in the evening and morning sun, on low dry boughs and shrub summits in the tops of the grass. The Crows hardly frequent the right spots at all regularly.

(ι) ALAUDIDAE and MOTACILLIDAE (Larks, Wagtails, and Pipits), and many PLOCEIDAE (Weavers).

These, with many other small birds that feed on and near the ground, will undoubtedly be too intolerant of attack.

(vii) *The land reptiles.*

There can be no doubt that the woodland tsetses will feed on snakes when they find them, for such instances have been recorded. They will probably feed on tree monitors and tortoises also. Llewellyn Lloyd appeared to find from his experiments that an exclusive diet of reptile blood was unfavourable

to *G. morsitans*, but Kleine, Roubaud, and others found exactly the same for *G. palpalis*—also under laboratory conditions—though it has been found in the field that reptiles are not only a favourable, but the main food for the latter fly.

But the density of the reptiles of the woodlands is insufficient to render it possible that they could contribute much to the support of a population of tsetse flies, while crocodiles tend to be important only in the rather larger rivers and lakes.

Summing up, it may be said that there is no mammalian group which can compare with the ungulates as a food for the open-woodland tsetses (*G. morsitans* and *G. swynnertoni*), and it is doubtful if any but the ungulates can support permanently a population of these, though something has still to be said on the night mammals.

Of birds it can be said, on the contrary, that if *G. palpalis* were able to adapt itself to them, and if they were to permit it, there are large birds in plenty, and numerous young in their nests, ready to the proboscis of the tsetse in the very feeding-grounds it uses to-day, even if its reptilian food animals were gone.

One of Carpenter's observations on the coast of Central Kavirondo is relevant here. At a cluster of rocks with shady bushes on a densely wooded rocky point projecting between belts of papyrus and forming a rallying ground for *G. palpalis*, out of the ten females and five males examined by him five females and one male, or 40% of the total, contained non-mammalian blood which appeared to be avian. "It is highly probable," Carpenter writes, "that the unusual proportion of females on this rocky point was due to their congregating there to obtain food from the birds on this islet, only separated from the mainland by twenty yards of water" (Carpenter, 1924–25 : 191).

To the remaining tsetses, birds are regularly available also under the two conditions just postulated in some of the places which these flies now use as feeding-grounds or seasonal concentration-sites. The fact that the tsetses may be found hungry where ground birds are abundant proves nothing. They may be found equally hungry under feeding-ground conditions with large game standing about; this means merely that the flies coming to feed have found man first.

Normally birds are little used by tsetses, but, as stated above, Johnson and Llewellyn Lloyd, with W. A. Young and H. Morrison, found avian blood in 17% of the flies examined in a spot whence ungulates had been removed, and Lloyd found 15% of non-mammalian blood in a place whence they had not. J. K. Chorley failed to note an increase in avian blood in connection with the operations against the game in Lomagundi, Southern Rhodesia (Jack, 1934). The scale of his investigation is not recorded or whether ground-birds were prevalent in the feeding-grounds. Whether Muscids of the size of tsetse flies can become adapted to feeding on birds, these latter being probably for the most part intolerant and their feathers obstructive, cannot be said without fuller experiment, but they obviously have not done so adequately in the area in which game has been shot in Southern Rhodesia. Further, many of the larger available birds are white—a colour unattractive to tsetses.

This sub-section simply summarises the result of a general survey of birds and bird-habits in their potential relation to the tsetse. Experiments lie in the future as regards each species of tsetse, separately tested.

(b) The relation of the density of *G. morsitans* and *G. swynnertoni* to that of the ungulates.

That the hunger of the flies rises and falls with the evaporation rate has been shown clearly by Jackson. That the density of the flies does the same, after a lag, has been shown by Nash. It has further been found that the evaporative power of the air is far more effective in determining the hunger of the fly and, subsequently, its abundance than is the abundance or scarcity of game. That a very small game population is capable of supporting quite a fair fly population was noted long ago by Lamborn and has been amply confirmed by ourselves. Nash has noted during four years' close observation that it is only the larger game movements that produce any change in fly distribution. Jackson, an equally careful observer, reported that game was scarce in most of the areas examined in the Nzega District where he worked for a considerable time. "There seemed to be no effect anywhere on the distribution of tsetse. About Ushirombo (in Kahama) game is exceedingly scarce; fly is abundant and sleeping sickness is endemic. The only common animals are baboons; old wart-hog and giraffe spoor were seen in two places, and a reedbuck was seen on the road at night. A few roan antelope are said to occur to the west. It is illustrative of the scarceness of the game that the zoologist was referred to a herd of eland some thirty miles away." Johnson and Rawson's conclusions from their precipitin tests, that the presence of large numbers of baboons in a locality provided a source of food supply for both *G. tachinoides* and *G. morsitans*, is recalled. To resume Jackson's report, "in and about a valley where the advancing fly is apparently beginning to establish itself near Masiliwa [where Jackson carried out close observations for over a year] the regular game appears to consist solely of a greater kudu and a duiker, and two rhinoceroses which occasionally visit it in the rains. Animals have never been seen there by day, as human traffic across it on numerous paths is considerable. Marked flies taken to this neighbourhood and released there remained for weeks, and from their condition it was evident that they found their food supply sufficient. The hunger of flies everywhere was found to be correlated with the evaporation rate, regularly ascertained by instruments. High evaporation in these areas was broadly correlated with the increased numbers of game animals visiting the water-holes, where the flies were daily examined. When game and evaporation both decreased, the hunger ratio (mean hunger stage) of the flies fell, showing that despite the departure of the game heightened humidity of the atmosphere sufficed to relieve the hunger of the fly, and showing also that a very small game population was adequate for the needs of quite a large fly population."

Similarly, with Burtt's observations at the Wa'amahla pools in Sambala. These were under intermittent observation by means of fly rounds from April 1928 to September 1929 and under observation twice daily from 1st June to 19th October, 1929. "During these periods the frequency of visits by animals varied greatly according to season, and it was hoped that a study of the game numbers would show correlation with the numbers of the relatively dense fly which used the valley as a feeding-site. A strong correlation with the evaporation rate was found, in that where this rose the numbers of flies at the pools would rise also relatively to those in the general woodland. This correlation appeared to swamp any correlation with game that might exist. Thus in the cold season following on the rains in 1928 herds of elephant and buffalo were drinking frequently at the pools from mid-June to July. Although fly numbers showed irregular and sometimes considerable fluctuation, they remained on

the whole low and the fluctuations could not be associated with the visits of the animals. Before the warm weather in August the visits of these large animals ceased, but wart-hogs and antelopes in very small numbers visited the pools throughout the dry season. The numbers of the flies became high (relatively and actually) in conformity with the known effects of the physical factors, but no correlation was established with the game."

In the following year the observational results followed exactly similar lines. These need not be quoted here in detail till we come to those for August. " A fire passed through on 1st August and the evaporation began steadily to rise. Fly numbers at once embarked on a marked increase, actual and relative. On the 6th August, luckily after the effect of the heightened evaporation on the flies had for a few days been observed, a herd of zebra began to drink at the pools, and continued to do so at short intervals throughout the period. On the 22nd August elephants also began to visit the pools, making eleven visits up to the 19th October when the investigation was closed. Wart-hog and occasionally roan antelope continued to frequent the place, but the fly numbers continued to behave in the normal way in association with the meteorological changes and not with those of the game. Similarly with the pools on the Mbuga Fly Round at Sambala."

A quotation from Nash will show that all three of our workers in different belts and localities of *G. morsitans* have been forced to the same conclusion (1933, *Bull. ent. Res.*, **24**: 136) :—

> " The Game Factor . . . is considered to be the least important of the three great factors—season, vegetation and game. Provided that there is a sufficient food supply, this factor ceases to be of interest; it is surprising that when game seems to be exceedingly scarce, fly continue to appear well-fed. Probably the ubiquitous wart-hog, which is a favoured host, is quite capable of supporting a fly community. There is no correlation between abundance of game and abundance of tsetse; on the contrary, tsetse is scarcest in the late dry season when game is exceedingly common, owing to the arrival of great herds of migratory game from the waterless Masai Steppe; fly is most abundant when game is relatively scarce and dispersed owing to abundant water supply." This is true of *morsitans* wherever we have studied it and of *swynnertoni* at Shinyanga, and is a true density effect.
>
> " Fly appear hungrier in the late dry season than at any other time of year, this being due to the high evaporation which makes them require food more often. At Kikore, provided that the food supply is sufficient (and very little appears to suffice), the game factor ceases to be of primary importance in the existence of *G. morsitans*. The effect of game upon the tsetse is only noticeable when large concentrations of game are taking place; these produce fluctuations in the apparent fly density and female percentage, but are of no practical importance. The convergence upon the watering places by game entering the fly belt attracts many fly into the neighbourhood of the concentrations " (Nash, 1933*a*).

Jackson (1933*c*) writes that " Broadly speaking, if food is adequate to support permanently a few tsetses it is adequate for any number. If food is absent or inadequate for a large population of tsetse, then not even a few can exist."

It will be seen from the above why the observations of past writers on tsetse on the subject of the relation between game density and fly density

have been thoroughly contradictory. The real key—desiccation, whether determined by measuring the evaporative power of the air or the saturation deficit—was missing. Nevertheless, it is suspected that, where a specially suitable food animal, such as is probably the buffalo (see the section on the rinderpest below), is readily available in great numbers and close concentration, the effects of desiccation might be mitigated for the flies that are living at the concentration. Further, it is suspected that a great fly population built upon contact with so favourable an animal might on its departure fail to be supported by, say, a few antelopes, not through shortage of blood or failure to find them, but through their being driven away by excessive biting.

(c) The possible effect of great numbers and high visibility of animals in lessening "concurrence requirement."

At Banagi on the Serengeti Plains, where game is enormously abundant in the open *Acacia* wooding, I found the latter in use by *G. swynnertoni* as, apparently, both breeding-ground and feeding-ground—even in the absence of thickets. The pupae were found under the smallest shelter beneath the roots of the trees, grass fires being also at their mildest owing to close grazing.

I found also a not dissimilar situation in Kilosa at a great dry-season game concentration with stamping-grounds. The tsetses were even breeding in the open ground at the latter, but with high mortality of pupae, doubtless from insolation.

In Block 5A in Shinyanga in 1934 a reinfestation by *G. swynnertoni*, caused by traffic in and out of the neighbouring block, assumed large proportions even in the absence of thicket. Cattle had been brought in and were being grazed daily in the fly area in very great numbers.

It appears likely that where blood can be obtained at any moment the need of the dense-shade element in the flies' vegetational requirements is reduced. This happens very rarely and very locally.

7.—THE PROBABLE RELATIONS OF THE TSETSES TO THE NOCTURNAL VERTEBRATE POPULATION.

(a) The nocturnal mammals.

(i) *The carnivora.*

A native woman in the village of Old Shinyanga, owing to a morbid appetite or being kept short of food, used to raid the larder at night. Later she was persuaded to sleep outside. The hyaenas, one night, in an access of boldness, seized her and dragged her off shrieking. According to eye-witnesses who ran out, a veritable troop of hyaenas was present, but one would drag the body along, then another—each, as the subsequent search suggested, till it had successfully bitten off or dragged off a portion. The last portion was finished a mile and a half away. I carried out a poisoning campaign on nine evenings thereafter, during which more than eighty pieces of meat poisoned with strychnine were taken. Owing to the long-grass conditions and lack of time and labour only five hyaena bodies were recovered, at distances up to three miles, but fully twenty must have died. Nevertheless it was calculated from the spoor that at least that number of hyaenas still visited this small station each night. Lombard used strychnine afterwards in Nzega, where hyaenas were destroying stock. With a large labour gang and conditions otherwise better for the finding of the bodies, he secured 52 in two nights at his camp. These figures are given to convey some idea of the enormous

numbers in which a single nocturnal species (*Crocuta crocuta*), rarely seen in the daytime except on open game plains, may be present. But far more striking than this were the multiplicity of paths, dissecting the grass in every direction and at the closest of intervals, that were found on planning the bait-laying; and the multiplicity and diversity of the spoor with which these paths were each morning engraved. Wild cats (*Felis ocreata* ssp.), genets *Genetta tigrina* and others), civets (*Civettictis civetta*), mongooses (of several genera), jackals (*Canis adustus* especially), fennecs (*Otocyon megalotis*), pied weasels (*Ictonyx striatus*) and *Poecilogale albinucha*) wander at night in far greater numbers than even the car headlights suggest, and their numbers afford some measure of the size of the rodent population that forms a part of their prey. In addition, lions and leopards, the other hyaenas and the Aard Wolf (*Proteles cristatus*), the Honey-Badger (*Mellivora capensis*), the Serval (*Leptailurus serval*), and the African Lynx (*Caracal caracal nubicus*) are all active at night.

(ii) *The rodents.*

In parts of the country the jumping hares (*Pedetes caffer*) are about in abundance at night; ordinary hares of the genus *Lepus* are much more in evidence by night than by day; and porcupines (*Hystrix africana australis*) often become active in some numbers. The remaining rodents are (visually) inconspicuous at night and have moreover been discussed on p. 209 above.

(iii) *The ungulates.*

An unexpected addition to the Shinyanga night population was the tree-coney (*Dendrohyrax stuhlmanni*),* an individual of which was found by Burtt in a small, standing hollow trunk knocked over during the clearing of the transects in 10A. Not known to occur outside a rain forest or nearer than those of Bukoba, this individual revealed the presence in the dry thorn savannas of the Territory of a population, probably small, of a species never seen there by daylight.

The ungulate population that is seen in the daytime moves also at night, with the large carnivora that prey on it, and in face of persecution becomes almost wholly nocturnal.

To what extent is the great nocturnal fauna fed on by tsetses at night, or found by these flies in the daytime?

(b) The night habits of the species of the *G. morsitans* group.

G. morsitans and *G. swynnertoni* are not usually nocturnal. In one of my experiments attack by *G. brevipalpis* and *G. pallidipes* on bait-animals ceased as soon as it became completely dark. In a more extended experiment by Nash on *G. morsitans* at Kikore attack on bait-cattle was not obtained at night. In an experiment by Vicars-Harris and Potts at Shinyanga *G. swynnertoni* attacked the observers by moonlight, but they thought that only those attacked which were disturbed by their passage through the grass. On the other hand, when once I was with a safari of about 25 porters and game scouts in the Handeni district, I sustained an attack by *G. morsitans* by moonlight in passing along an open road in miombo, though with longish grass at the sides. When these flies attack man at night they do so in a normal manner and are obviously in full use of their senses. Whether, like their ungulate prey, they are capable of becoming more largely nocturnal is unknown and can only be proved by experiment, but from the Rhodesian game experiment this seems doubtful.

* Identification confirmed by the British Museum (Natural History).

Of *G. pallidipes* my observations in Portuguese East Africa suggested that, like *G. brevipalpis*, it probably to some extent hunts by moonlight. Actual attacks were experienced.

(c) The night habits of *G. brevipalpis* and *G. longipennis*.

So many instances have occurred in the course of our work in which *G. brevipalpis* in some numbers has come into the camp at night, that it has been difficult to resist the conclusion that this species, crepuscular in any case, probably hunts also by moonlight. The flies have not gone to the lanterns but have settled on the lighted under surfaces of our tents.

G. longipennis has been recorded (Neave, 1912) as coming constantly at night into the trains between Voi and Makindu.

(d) The extent to which the nocturnal mammals may be utilised by the tsetses.

The night population described above wanders along tracks in the grass or traverses the latter without them. Flies may thus be disturbed and, to judge from the observations quoted above, may attack the larger animals at least and get feeds. Apart from the fact that some of these may (like the cheetah) be unacceptable, it seems unlikely that disturbance as a source of food is important at night to the species as opposed to odd individuals. To *G. brevipalpis* and possibly to *G. pallidipes*, hunting their food at night, night mammals may be important.

Further, the flies may find the strictly nocturnal animals lying up during daylight. The hollow trunks to which genets and tree-hyraxes retreat are amongst the places most used by the tsetses for larvipositing; burrows attract them, and the fact that Jackson has found rot-holes as high as 9 feet from the ground being freely utilised for breeding by *G. morsitans* suggests that bats might be attacked, though a limitation referred to above would be present, viz. that these places are used by the fed, and not by the hungry, tsetses, not but what they might feed on the animals as hunger returned. Fruit-bats, as there stated, hang up in the foliage, often at no great height and in very large numbers indeed. I have recorded a case in which many *G. brevipalpis* and some *G. pallidipes* had found and were feeding on a pair of bush-pigs asleep in very long grass which precluded lateral vision under "home," not feeding-ground conditions, showing that they will use animals in the "home." They might equally find hyaenas, and jackals are commonly seen at large during the hours of the activity of the tsetses. Harrison, in Block 9, watched two hyaenas (*Crocuta crocuta*) enter by daylight a strip in which tsetses were especially abundant. Their movements (tail-lashing and snapping back at themselves) at once suggested attack by tsetse; so probably they are not avoided, and in fact hyaenas are amongst the mammals in which trypanosomes have been found.

On the other hand, susceptibility to artificial infection of the very small night mammals may argue that not many of these are attacked by the tsetse. The turning of attack on to them might cause mortality, reduction, and thus unavailability. Some will be capable of dealing with attack. As regards regularity of movement and use of recognisable paths, the night mammals yield nothing to the ungulates and should be all that a night tsetse could desire. Tsetses hunting in the daytime will chance on them lying up, rather than be able to count on them.

The detailed work on this subject still lies before us, but it has been considered worth mention in view (*a*) of the great size of the night population;

(*b*) of the fact that some tsetses are probably partly nocturnal, while the others may find an incidental source of food in the night mammals lying up in the daytime; and (*c*) of the possibility, therefore, that some of the night vertebrates proper might in some areas play a part were the ungulates to be exterminated. Our game experiments (*see* pp. 282–291 below) should throw light on this possibility, as also on the usefulness or otherwise to the separate species of tsetses of the ungulates when they are made wholly nocturnal. Jack's work goes to show that they are not then of much use to *G. morsitans*.

8.—THE EFFECT OF RINDERPEST ON THE TSETSES.

(a) Rinderpest and *G. morsitans* in the Transvaal.

I paid a brief but most interesting visit in May 1931 to the Kruger National Park, where I was the guest of Colonel Stevenson-Hamilton, the senior and best known of Game Wardens. This Park occupies a part of the Transvaal which before the great rinderpest plague was infested with *G. morsitans*. The history, as given me very kindly by Colonel Stevenson-Hamilton, was as follows :—

Up to 1858–66 the country generally was very heavily settled with natives, and it is probable, if not certain, that apart from the question of the natural distribution of suitable bush, this was responsible in the first place for the patchy and separated nature of the fly belts on both sides of the Portuguese border that was later noted by Europeans. The years mentioned were occupied with the devastating civil war between the two Zulu brothers Umzila and Mawewe, claimants to the Shangan Chieftainship. This had barely ended when an era of very heavy killing of game took place, beginning in 1870 and continuing, on the part both of Europeans and natives, up to the great rinderpest in 1897. When it came, impala still survived in some numbers but had taken to the dense thickets; eland were greatly reduced already, and about 200 buffalo, it is believed, were left in the Sabi area. The rinderpest killed kudu, eland, and wart-hog, and reduced the 200 buffalo to 15. It spared amongst others the impala and waterbuck. This was the position when Colonel Stevenson-Hamilton arrived five years afterwards.

Motoring through the Park with him it struck me that a great proportion of the country that we were passing through was of the *Combretum apiculatum* (or *Zeyheri*) type which elsewhere, if in bulk, is evacuated by *G. morsitans* during the late dry season. I was eventually able to point out a piece of country which was likely to hold the fly all the year round. It was a shallow drainage valley characterised by *Acacia pallens* and *Albizzia hypoleuca*, with water-pans and clumps of large trees that would be evergreen or nearly so. "That is particularly interesting," Colonel Stevenson-Hamilton said, in effect, "for these places are the special buffalo haunts and it was in these that the two hundred buffaloes persisted until the rinderpest destroyed most of them." He roughly estimated the total of the suitable area in the Park (which is as large as Wales) at only 20 square miles.

There is no need to labour the inference, and it is possible that a study of the vegetation of the sites of these Transvaal and Portuguese belts by someone very thoroughly conversant with the habits of *G. morsitans* under all kinds of conditions might strengthen the suggestion that it was a special and essential association with buffalo in the fly's dry-season haunts that led here to the insect's undoing. It will be remembered that this animal, but not all the rest of the game, was almost exterminated by the rinderpest in these small

separated fly belts after twenty years of intensive game killing in bush which had previously been broken up greatly by settlement and which in any case must have been near the climatic limit of *G. morsitans*. The explanation does not, however, apply equally to the great Rhodesian belts evacuated at the same time.

(b) Rinderpest and *G. morsitans* in Uganda.

Duke (1919) investigated a rinderpest outbreak which passed through the Masindi Port country of the Northern Province of Uganda in 1917. This country carried heavy grass, 6 or 7 feet high in its season, and was one of those areas which is characterised by the concentration of *G. morsitans* in separated primary foci in the dry season. The details are summarisable as follows :—

(i) The area was investigated by Fiske and Duke in May and June 1914 and the flies found to be "fairly numerous throughout the area, especially along the various roads."

(ii) In early 1917 cyclists were still being worried by the flies on the road.

(iii) The highest monthly rainfall in four years took place in September 1917, but whether well distributed or in part as a deluge is not shown.

(iv) Right through the long grass season the game was dying in numbers throughout the fly area as the result of rinderpest in 1917. In November the outbreak was still in full swing and Mr. Bain, District Engineer, was struck by the absence (already) of flies on the road.

(v) In November also the "exceptional drought" began, the intensity and prolongation of which in that year led to an unusually complete burning of the bush.

(vi) Neighbouring areas to which the buffalo fled when attacked by the disease were Buruli, south of the Kavu, and Bugungu.

(vii) Duke investigated in April 1918.

He found, as regards the game, that the buffalo, bushbuck, duiker, and wart-hog had died in large numbers. The last three were regarded as locally the most important: "elephant and buffalo come and go." Waterbuck and hartebeest were little affected. As regards the flies, there was a strong differential result as between the three areas concerned. There was evident "a marked diminution in the numbers of *G. morsitans* in the Masindi belt. . . . The fly is not exterminated, but the reduction in numbers is much more marked than that which ordinarily results from the annual hot season. In Bugungu the reduction, if such has occurred, is less apparent. . . . In both areas considerable quantities of waterbuck have lived through the epidemic. Buffalo have also survived in some numbers, though, on the Bugungu plains especially, the number of dried carcases testifies to a heavy death-roll." "It appears that fly are more numerous in Northern Buruli than they were in 1914."

Duke writes further: "The drought, beginning in November, led to an early drying of the grass and commencement of the fires. Similarly the intensity and prolongation of this drought led to an unusually complete burning of the bush. The fly were thus doubly handicapped. Firstly, their food supply was diminished at the most critical season of the year; and secondly, the adverse conditions of deprivation of shelter and destruction of breeding-grounds were intensified by the prolonged drought." Elsewhere he refers to "the arrival of the disease in the district at the season of the year when the grass is up and game most difficult to find." He concludes: "I consider that

these phenomena afford a reasonable and probable explanation of the remarkable diminution in the numbers of tsetse in the Masindi fly belt. The Bugungu country, being uninhabited, is less subject to burning in the dry season" (1919, *Bull. ent. Res.*, **10** : 19).

There is no reason why this conclusion should not be correct. At the same time it should be pointed out (*a*) that this long grass country "with scattered small trees and bushes rising above the coarse grass" is not, by us, regarded as the most favourable to *G. morsitans*; it is country from which the species might recede cyclically or from small causes; and (*b*) that the exceptional grass-burning recorded for 1917 might, on our experience, easily alone have produced the reduction referred to in this type of country; in Bugungu, less thoroughly burned, reduction of fly was non-apparent, and that some at least of the surviving *G. morsitans* in Masindi were keeping well in touch with the game is shown by an instance given.

As part of the same investigation Duke usefully proved that rinderpest blood "exercises no apparent effect on the fly. It was impossible to pronounce decisively regarding the effect on larva production."

In the outbreak observed by Kennedy (1929) the buffalo lost "very heavily, but deaths amongst the bushbuck and pig also occurred. . . . The hartebeest, waterbuck, oribi and duiker, also elephant, white rhinoceros and hippopotamus were unaffected by the incidence of the disease." It is obvious from Kennedy's description of the numbers in which buffalo occurred in the new game-fly concentrations that followed, that even the animals affected were far from being so nearly exterminated as in the great epizootic of the early nineties, but the details are of definite interest.

I myself have observed that "the buffalo covers, with its great herds, very large grazing grounds, is continually wandering back and forth between its various centres . . . and breaks up into parties and individuals that leave little ground in the general range unvisited in the rainy season" (Swynnerton, 1921 : 342). Kennedy supplements this description of the position when buffalo is inordinately plentiful by describing what happens when it is made less abundant. This species, he says (p. 14), "is naturally a dweller in dense cover near water, but when increase of numbers occurs and an area is, so to speak, saturated with buffalo, then considerable numbers are forced to live in the open country, under relatively unsuitable conditions. . . . Consequently the decrease in the buffalo will be more marked in open bush country than in the dense coverts, as losses in areas of the former description will be accentuated by a movement of the survivors" to the riverside covert "which will replace to a certain extent the losses in the latter."

Thus, actually, in the west Nile outbreaks, the buffalo disappeared from certain more open areas but, with other important game animals, remained abundant in the favourite coverts. Oribi, waterbuck, hartebeest, duiker, buffalo (now not numerous), white rhinoceros, kob, carnivora and small mammals, were still found in the more open areas three years after the outbreak, but the flies "were absent or found in very small numbers" and showed the high female proportion that is associated with country which hungry flies enter for food. Evidently feeding-grounds had been partially abandoned with their evacuation by the buffalo, though the other animals remained.

(c) Discussion of the problem.

This contraction of the distribution of the feeding tsetses in sympathy with that of the buffalo, while merely a move in "find-the-new-game-con-

centration" which is the life-long puzzle of the tsetse and is seen taking place all the time in sympathy with the larger game movements in the areas that we study, adds to the impression (still to be confirmed scientifically) that was gained by the pre-1896 hunters and by myself in Portuguese East Africa and at Kilosa that, while the flies flourish well on other game species, the buffalo is nevertheless a specially favoured food animal and one to which the flies become particularly attracted and adapted, acquiring great density in contact with it in the thoroughly suitable surroundings which it so commonly frequents. To the buffalo, may be added as favoured hosts the pigs (wart-hog and bush-pig). Undisturbed buffalo, at their dry-season concentration sites in suitable country, are an ideal host for the tsetse, their habits are absolutely regular and dependable—as are those of the pigs—they graze in the vleis morning and night and lie up in the rest-haunt and thickets. They are often also in very great numbers. The placid tolerance of the buffalo and pigs, and probably a high suitability of the blood, would also contribute to this result. On the disappearance of the buffalo, coupled with that of the wart-hog, flies specially adapted to them might not immediately adapt themselves completely to the habits of the other large mammals, particularly if these were not abundant.

If there were such a slowness to re-adapt, it would form a part of the explanation for the disappearance of the flies from some of their ranges at the time of the epizootic of the nineties, when, as on the west Nile in 1925, only certain game animals were affected. It would be by no means a complete explanation, for the young flies, emerging from the pupae, would hardly inherit the attachment. Why did they not continue to live on the species that remained? Actually on some of their other ranges, though the destruction of the same dominant game animals was apparently equally severe, the tsetse remained for practical purposes unaffected. I lived beside the *pallidipes* area in Mossurise in Portuguese East Africa and hunted in its *morsitans* area four years after the great rinderpest. Buffalo, formerly abundant, had almost completely disappeared. There was plenty of other game, such as Lichtenstein hartebeest, waterbuck and oribi; and odd duikers were noted as present at the concentrating grounds of the flies. No density counts were taken, but, from memory and judging from diary entries, the flies were just as abundant as they were found to be in the same month eighteen years later, when the buffalo had recovered, nor were their boundaries less.

The following theory would contribute to the covering of the facts. Buffalo herds under attack from rinderpest tend to quit the locality in which their companions are dying and to leave it completely deserted so far as their species is concerned. Pig and certain antelopes are also destroyed. The latter as a whole, and hartebeest in particular, are much more intolerant of attack by biting flies than are pig or buffalo, and the sudden and unaccustomed concentration on them of vast numbers of tsetse, hitherto battening on buffalo and pig and a larger population of game generally, might have driven them out of the foci. The fewer they were, or the more numerous the tsetse, the more likely would this be to happen. A differential result as between different fly ranges would thus be contributed to.

Two other factors would be still more important—the type of country and (as Jack and Duke also suggest) the time of year. Where suitable sites were as abundant as at Sambala and the country between as traversable, their hunger would scatter the flies and many might again find game with localised habits. But in country in which the flies had had to concentrate closely in the dry season or permanently in sites somewhat far apart, especially

if these sites were the concentration sites also of great numbers of buffalo, catastrophe to the animals might involve also the tsetse. It would do so chiefly if it included the time of year—late dry season—which through the impassability to the flies of the intervening country at that time, would preclude the scattering of the flies to find new hosts and new game-concentrations, or at least kill those which scattered equally with those which remained.

If it was only the great numbers of the animals previously present that had made the concentration sites primary foci, in the subsequent year also any offspring that survived through the rains would in the dry season be stranded also. In areas in which the focus sites generally offered no great advantage one against another, a reduced game population, incapable of populating all, might be attracted to different sites each dry season through a differing annual location of attractions—as early grass, depending for its incidence on that of burning and showers—and might thus bring about an extermination of the flies which it might take some years to complete.

Add, finally, Jack's observation (1919) that " under persecution game develops a habit of visiting the vleis at night and leaving at dawn, so that the fly does not get the same opportunities for feeding. It is conceivable that the great losses amongst the game during the rinderpest may have produced a similar shyness. . . . During the wet season the presence of only a fraction of the usual food supply scattered throughout the forest would in any case have a very deleterious effect." He also stresses the probable effect of shortage of food on breeding.

The above still would not account for the evacuations which took place before the rinderpest or the smaller recent disappearances in Tanganyika. In the Transvaal, " while tsetse remained abundant in the low country between the Drakensburg foot-hills and the Lebombo range down to the time of the rinderpest, it had disappeared before that epoch from two-thirds of the Territory it previously infested " (Fuller, 1923). Again, half of the great *morsitans* belt on the Limpopo, characterised by mopane wooding, had already disappeared, according to Selous, before the rinderpest, and Marshall states that ox waggons were regularly traversing it in 1893 (Jack, 1914 : 100, editorial footnote). The fly belt west of the Victoria Falls had gone by 1888. There is more doubt with regard to the belt to the east. I do not know whether any pre-rinderpest rainfall records are available from the Limpopo area. At any rate it would seem that in none of the areas that disappeared here before the rinderpest was hunting sufficiently intensive to account for it.

Nash, as the result of the wholesale destruction of *G. morsitans* by a ten-days deluge of rain in Kikore in 1930, questioned " whether some of the sudden disappearances of fly that one reads about may not have been due to abnormal rainfall." Judging from what happened in and west of Sambala in the year of downpour which Nash had in mind, abnormal rains are unlikely to have been the cause in the Transvaal; for a great part of the country referred to by Fuller is, like Sambala, well-drained. Continual harrying of the game by numbers of resident settlers, such as would have prevented it from forming regular habits and the flies from regularly finding it, might well have contributed here, where the fly belts were in any case diminutive; but that *G. morsitans* should disappear from country in which it was intimately based on mopane wooding (as it was in the Limpopo area) as the result of an intense rain-deluge could be just understood. Knowing both, I consider that the wet-season conditions in the mopane resemble sufficiently those of the *Acacia–Combretum*-covered plain below Kikore. But flies should in any case have

survived at the contacts with the better drained wooding so that flooding again might be regarded as liable to be a contributory cause only, producing the instability in a *morsitans* belt that elsewhere may be produced by long grass. The Salisbury rainfall records, quoted by Jack, show December 1895 (12·88 inches) and February 1899 (18·79 inches) as the months of high rainfall in the period concerned.

(d) General conclusions.

The following conclusions emerge from the foregoing discussion :—

(i) Some fly belts (Southern Rhodesia, North Basutoland) decreased vastly in size or (having been very greatly reduced previously, like those of the Transvaal) disappeared finally at the time of the rinderpest.

(ii) Other fly belts appeared unaffected or only slightly affected (Mossurise, Tanganyika Territory, Nyasaland, at least much of Northern Rhodesia).

(iii) Other fly belts—and fairly large ones—had already disappeared before the rinderpest (at least on the Limpopo), as the result, apparently, not of such game destruction as could, in my opinion, affect them.

(iv) Instances have been seen since (Tanganyika) of small retirements of the flies that seemed dependent on seasonal cycles, and temporary abandonments of country unconnected with the game factor. An instance has been noted in which abnormally concentrated rainfall destroyed temporarily a low-lying section of a fly belt. Plagues of Asilid flies, which coincided with the disappearance of the tsetses, have been suggested as being responsible for other instances.

(v) The rinderpest killed only certain species of game, while others remained in numbers.

(vi) Probably the rinderpest contributed to the reduction of the belts that were reduced coincidentally with it. It is thought possible that it operated partly through the destruction of the pigs and buffalo, both specially favourable food animals, combined with a difficulty on the part of the flies on the wing in re-adapting themselves to new animals, and with an expulsion of other game species from fly foci by the concentration in them of large fly populations, the attacks of which were previously distributed over a far greater number of animals; but it is thought likely that in each case some special factor must have been present additionally without which disaster to the tsetse could not have occurred.

The following factors are possibilities :—

(*a*) In the Transvaal generally, owing to the small size of the areas and to their wide separation, any disaster or even an unfavourable weather-cycle might have deleted them, once thus separated. In Tanganyika the areas since evacuated by the flies were re-stocked automatically, as they were still attached to main belts. In the Transvaal, this was impossible. Quite likely the persistent and long-lasting harrying of the game that followed European settlement contributed to the expulsion of the tsetses from the two-thirds of these areas that were freed before rinderpest came. Moreover, the mere presence of the various activities of man in some numbers seems inimical to *G. morsitans* (see pp. 291 and 325 below).

(*b*) In the large Limpopo fly belt, quite half of which, according to Selous, had gone before rinderpest came, and this not, it is thought, through hunting

intensive enough to account for it, abnormal rainfall is a remotely possible cause, for the fly bush was mainly mopane on ground liable to be swamped in a deluge; but complete extermination from this cause is unlikely, for flies should survive at the contacts with better-drained wooding.

(*c*) Other characters, such as very long grass, which, through liability to heavy fires and the humidity effects of exceptional rains would render infestation unstable. Probable instances are provided by Masindi in Uganda and by part of Handeni in Tanganyika.

(*d*) Coincidence of the epizootic with the long grass season followed by exceptional fires in the late dry season in a year of special drought (Duke 1919). In few *morsitans* areas is long grass a general feature, but the second factor could be fairly widely effective.

(*e*) In the limited part of the Kruger National Park that I saw, the very small area that could have been used for seasonal concentration and the extreme dry-season inhospitality of the country between such sites. Small availability of game in the country between when the rinderpest came, and a special association of the flies with the 200 buffalo that it decimated in concentration grounds common to both the latter and the flies. The coincidence of the rinderpest with the dry season, as Duke has suggested also.

(*f*) Probably in much of Rhodesia as well, wide separation of permanently suitable fly centres; the country between them inhospitable either in itself (as miombo wooding on Kalahari sand) or through dry-season conditions at that time. When, stricken with rinderpest, the pigs died, the buffalo died and deserted, and game numbers generally were reduced, the flies, perhaps driving the surviving game out, may have been left stranded for a longer period than covered their hunger-cycle and the pupal period and hunger-cycle of their offspring.

I doubt if the rinderpest was wholly responsible for the results that have been attributed to it. The fact of previous and subsequent abandonments of country by the tsetse tells against it. But in the various special circumstances suggested it might have acted as is here sketched.

As regards our ability to emulate it, Jack wrote in 1923 of his game destruction experiment: "At the commencement . . . it was thought that a similar phenomenon might be brought about by a sudden and intense onslaught on the game within the limited area selected. This did not occur, however, and the difficulty of eliminating game within a limited well-watered area, adjacent to heavily stocked game country, is one of the important lessons learnt." Over the course of a number of years, the game was sufficiently reduced. An experiment on an isolated concentration site figures in our programme for Tabora.

9.—THE POSSIBILITY OF EXTERMINATING THE FOOD ANIMALS OF THE TSETSES TO THE POINT OF EXTERMINATING THE FLIES.

(a) Food animals of *G. palpalis*.

It is probable that an intensive campaign against the crocodiles and hippopotami of Lake Victoria would be moderately successful in so far as their destruction is concerned. The monitor lizards, more important as a food of the fly, would remain and might be more difficult and expensive to deal with, though their skins are in demand by the natives for making drum-heads. The destruction of the crocodiles might possibly react on the lizards, as they live so greatly on crocodiles' eggs, but being omnivorous and much other food

being present, they might actually be little affected. Further, being the chief enemy of that pest, the crocodile, their protection in this connection would seem more important than the problematical effect their destruction might have on *G. palpalis*.

(b) Food animals of *G. morsitans*.

After eleven years in game work and fifteen on tsetse research in Tanganyika, I still hold the view which I expressed at the outset of the work (Swynnerton, 1921). This ran as follows : " In a relatively clean-stemmed area . . . it is to me very conceivable that wholesale game destruction might banish the fly. An obstacle, however, would be that the whole territory is one vast game area, so that the game would pour again into a given section of it as soon as the persecution was relaxed—unless an effective barrier were created such as could probably only be made a permanency with settlement behind it. Whether the returning game would bring fly in again would depend on (i) whether the whole continuous fly area had been cleared of fly, or (ii) whether the portion cleared had been split off from the uncleared portion by an effective barrier against the fly itself."

Where " the country is much more jungly, wholesale game destruction is proportionately more difficult. In addition this country abounds in bush-pigs, which are difficult to destroy and which in anything approaching their present numbers can probably alone support the fly, with baboons, abundant cane-rats and other animals which may all contribute to its sustenance. I consider that it will be impossible to starve the fly at all generally by ordinary game destruction here, at any rate before the country is very fully settled." The country referred to was Mozambique but the remark applies to the rest of east Africa also.

Confirmation of this view is forthcoming in the fact that in Southern Rhodesia game destruction in the thicker country produced its effect with more difficulty (Jack, 1923 : 70), but when persistently carried out in more open savanna wooding was in the end successful (Jack, 1923, 1934). It should be noted, however, (i) that game destruction has to be very intensive and persistent to be useful ; (ii) that it cannot be brought about in sufficiently radical form by the intermittent methods of a native population left to itself, since it relaxes its hunting when the game becomes scarce or neglects the nearer game for the further where the latter is denser or more prized, and in Mohammedan country neglects the pigs altogether ; or by merely throwing country open to free shooting by Europeans or employing native hunters without European supervision ; and (iii) that as carried out by the Southern Rhodesian Government on the only lines on which it can succeed—as a highly organised measure by paid men—it is expensive over any considerable area and is also, admittedly, a permanent commitment for the reason given above—that the game pours in again. Jack argues, however, that the annual expense capitalised is not excessive for the object in view in Southern Rhodesia.

Some quotations from Jack (1933–1934) will be of interest : " Since the cordon was completed . . . no appreciable amount of ground has been lost . . . and ground has been definitely gained in various sectors (1934). . . . Before the completion of the cordon the operations were controlled from an experimental standpoint by the sectors on either side, where, in each case, the fly's advance continued if the country were suitable. . . . The measure is, of course, not practicable under all conditions, nor would it be effective against certain species of tsetse flies. . . . Complete extermination of the larger

mammals over any extensive tract of country is impracticable. The big game and even the wart-hog may be got rid of, but small buck are not easily eradicated, whilst baboons, bush-pig, etc., will certainly remain in some considerable numbers if the country is favourable to them " (p. 19).

" Game still remains. Under persecution the game tends to return to the hills or into the less open forest during the day and to come down to the grazing grounds after dark, leaving again before sunrise. Under these circumstances the fly, which is diurnal in habit, is not in a position to make the best use of even the reduced amount of game remaining. . . . It is judged that this development is a potent factor in enhancing the effect of game reduction by hunting methods " (p. 31).

" It takes several years under the most favourable conditions to bring about any considerable and definite *retrogression* of the fly, but this follows in due course if the zone is wide enough. . . . A twenty-mile-wide zone is now considered to be necessary " (p. 32).

" For a period after operations . . . have been inaugurated, trypanosomiasis . . . is liable to occur further afield than previously. This is almost certainly due to the wider ranging of the hungry flies through game-depleted country. It is a temporary phase only " (p. 33).

" The comparatively slow rate of fly reduction is apparently due to (1) constant invasion [by flies] of a portion of the zone from the country beyond; (2) incomplete removal of the larger mammals; and (3) occasional feeds obtained from sources other than the larger animals " (p. 32).

" The main objection to the present measures, apart from their general distastefulness, is the lack of finality in reference to results. Obviously operations will need to be continued indefinitely to maintain the position or to reclaim new ground " (1933 : 12).

" The present distasteful measures would certainly not be adhered to in the event of any feasible and equally effective alternative being discovered."

Certainly no one should wish to destroy the splendid game fauna of Africa, and no government to lose the revenue to be derived from licences and tourist attraction, if the object of eliminating the tsetse can be attained without.

Further, I consider that in a very great proportion of our fly belts in Tanganyika, as in the Abercorn belt in the north-eastern part of Northern Rhodesia, visibility, far poorer than in the savanna of Southern Rhodesia, is not sufficiently good for measures against game to be successful for our object.

(c) Food animals of *G. swynnertoni.*

A great proportion of *swynnertoni* country is of the types which Jack found difficult in Southern Rhodesia, through distances between water and density. It is very different from the open and thicketless wooding of so much *morsitans* country, much thicket and innumerable dikdiks are present, and generally the position in relation to the possibility of game extermination is different. Whether game disturbance will affect it, remains to be seen. An exploratory experiment in food-control in connection with *G. swynnertoni* is nevertheless of importance and that which is already in hand is described on p. 282 below.

(d) Food animals of *G. pallidipes, G. austeni,* and *G. brevipalpis.*

It is believed that in the average east African range of any of these species attempts at food-animal destruction will be a complete fiasco, and that the flies will remain quite unexterminated by such destruction as can take place. In this connection it may be remembered (i) that *G. pallidipes* is capable of

continuing to infest great pieces of country in very small numbers indeed; (ii) that despite their feeding so largely on pigs, these species have not, so far as we know, been in any way affected by the various rinderpest outbreaks, since in Zululand *G. pallidipes* continued when *G. morsitans* in the Transvaal disappeared and the Gazaland *G. morsitans* persisted; and (iii) that, between them, these three flies cover most *swynnertoni* country and quite half of that which is occupied in Tanganyika Territory by *G. morsitans*.

10.—GAME CONTROL IN RELATION TO TSETSES BY MEANS OF THE CONTROL OF COVER.

We are only at an early stage of our observations on this subject. Measures directed towards the production of more open woodland (as by organised late grass-burning) will probably effect little beyond changes in predominance of species, as a number of our commonest game animals are capable of living fairly indefinitely in such woodland and in fact resort for long periods to the more open country for visual protection from carnivora, if not for escape from the flies. The experiment in Block 4A in Shinyanga in the densification of the cover, by not burning the grass at all, gives the result " fewer impala, more greater kudu, but, still, plenty of game." The kudu may be regarded as the representative of quite a number of ungulate species that will gratefully use denser cover, but few of them like dense cover only, and the latter, disliked also by the tsetses where it stretches unbroken, is likely in any case ultimately to interfere with the finding of the animals by the flies. Cover control is likely to affect the flies more directly than through its effect on the game, though this may come into the picture.

11.—SUMMARY OF CONCLUSIONS.

To sum up, tsetses of both sexes depend on blood for their meat and drink and probably on nothing else. Certain species (*G. palpalis*, *G. tachinoides*) feed mainly on reptiles or man, *G. morsitans* mainly on game animals, and the rest at least largely on game animals, though their full food range needs study. Some species of animals are liked much better than others, and man is not a favoured food species, though he is more so with some tsetse species than others. Different preferences are shown by the different species of tsetse and a study of these preferences has been begun, which suggests that some mammals may be completely avoided. Quite inconspicuous animals are frequently fed on (such as monitor lizards, tortoises, and snakes); bird blood has also been found in a small proportion of the tsetse stomachs examined, and numerous large birds exist near enough to the ground to be of possible use to the tsetse, and on ground searched for food by the tsetse. It seems unlikely, in the case of *G. morsitans*, though mainly from the Southern Rhodesian experiment, that either these or the smallest animals and the nocturnal mammals could at all replace the game animals, whatever may prove to be the case with regard to other tsetse species.

Under undisturbed conditions a very minute game population indeed is capable of supporting a considerable fly population, and the senses and methods by which the flies that lose contact after each feed resume contact with the animals after the few days' interval required for digestion and seclusion, are discussed. Sight is very important. Scent for certain species is probably hardly less so: this is still under investigation. Hunger (still under undisturbed conditions) is produced less by scarcity of food animals than by high saturation deficit in the atmosphere—or, from another angle, by the evaporative power

of the air. Nevertheless, it is possible that if such highly favoured animals as the buffalo, which could assist in the building up of a specially high fly density, were killed off by rinderpest at the dry-season concentrations of the flies in country otherwise inhospitable at that time of year, this might destroy *G. morsitans* in those special areas, but not, so far as is known, any of the other species under their normal conditions. The conditions under which each species can or cannot be destroyed through game destruction is discussed, and the results of the Southern Rhodesian experiments, successful in open savanna woodland but with drawbacks as regards the need for indefinite upkeep and general applicability, are quoted. Our own experiments in game control and the possibility of employing cover-control in this general connection are referred to.

That limited game control, well-sited and timed, at key points in limited localities and under strict expert supervision will be necessary as part of our local combinations of measures is exceedingly likely. Our own observations so far have been all on undisturbed game; the effect of disturbance remains to be tried by us under scientifically controlled conditions, and the experiments to be described on pp. 284–291 below are planned to ascertain whether and where it will actually be useful and what form it should take. An ultimate need for widespread exterminative measures is by no means anticipated, nor could such be generally successful.

Q.—THE RELATIONS OF THE TSETSES TO THEIR ENEMIES AND OF THESE TO EACH OTHER.

1.—INTRODUCTORY.

The main known enemies of the tsetses are sixteen or seventeen species of pupal parasites belonging to six Hymenopterous families and one of Diptera, and the following predators: dragonflies (*Cacergates leucostictus* is of special importance on Lake Victoria), robber-flies (ASILIDAE), certain wasps (*Bembex*), spiders, and certain birds. The common drongo, fly-catchers (*Bradornis* and *Melaenornis pammelaina*) and bee-eaters have been watched eating tsetses, and Newstead and Davy took tsetses from stomachs of the common drongo (*Dicrurus adsimilis divaricatus*) and the little bee-eater (*Melittophagus pusillus meridionalis*). From observation of their detailed habits it is thought that birds that scratch up the ground for their food are certainly enemies of the pupae.

The mean length of life of male tsetse in the field was found generally not to be much more than six weeks. The rate of breeding in these insects being very low, it was suggested by Jackson that predators could account for very few, as otherwise the tsetse could not survive. Carpenter, earlier, had made a similar suggestion with reference to the low birth-rate. Now, however, it appears from our observations that females live much longer than males in the field, a hypothesis which allows room both for considerable destruction by predators of adult males in particular, and for destruction of pupae of either sex.

2.—ENEMIES OF THE PUPAE.

(a) Parasites.

Against one of the most prolific of the pupal parasites (*Syntomosphyrum glossinae*) the tsetse is protected by the habit possessed by its larvae of burying

themselves before pupating. *Syntomosphyrum* has proved a poor burrower except in humus, and in Musoma it is not a formidable enemy even then. A list of the parasites known up to 1922 is given by Austen and Hegh (p. 131), and by Hegh (1929 : 691–695). To this last may be added Herbert Lloyd's new discovery, *Arbothropria lloydi*. The full list for Tanganyika so far is :—

Parasite.	Host.	Locality.
Hymenoptera.		
Arbothropria lloydi Ferrière.	*G. palpalis* and probably *G. brevipalpis*.	Musoma.
Syntomosphyrum glossinae Wtst.	*G. morsitans* and *G. swynnertoni*; *G. palpalis* in the north of Victoria (Carpenter).	Kondoa and Shinyanga.
Stomatoceras micans Wtst.	*G. morsitans*.	Kondoa.
Stomatoceras sp.	*G. swynnertoni*.	Shinyanga.
Diptera.		
Thyridanthrax abruptus Lw.	*G. morsitans* and *G. swynnertoni*.	Kondoa.
T. lineus Lw.	*G. morsitans*.	Kondoa.
T. argentifrons Austen.	*G. morsitans* and *G. swynnertoni*.	Kondoa.

(b) Predators.

The many birds that scratch up the ground in thickets for their food—such as the ground-bulbuls (*Phyllastrephus terrestris* and others), the babblers (*Turdoides* and *Argya*) and the guinea-fowls and francolins—must, one supposes, find and eat numerous tsetse pupae, though they may not be searching for them primarily. One has sometimes found the carpets of thickets, the breeding-places of tsetse, so completely scratched up by guinea-fowls that it is difficult to believe that they do not account for tsetse pupae. On the other hand, one can work through considerable areas containing quite populous breeding-sites and find little evidence of bird attack.

"A more interesting observation was made on an elephant-shrew [presumably *Petrodromys tetradactylus*, that being the common local species] in a dry but shady donga entering the Buzi at the south end of the Sitatongas. We had searched for and found pupae (*austeni*) under a larger fallen tree and, going on to search under other logs and stones, found we had been anticipated by a small animal. For a distance of 47 paces along the donga every hiding-place that would have been used by tsetse had had the surface soil scratched out and the spoor and the droppings were, I should say (and the natives also were certain), distinctly those of one of these elephant-shrews. I have actually watched the above elephant-shrew in the wild state scratching thus for slightly buried insects and, having kept individuals in captivity, am familiar with their droppings, etc." (Swynnerton, 1921 : 369). These shrews follow the same beat with the greatest regularity daily and might well, on that beat, find and devour pupae. There is some evidence now in Kakoma that losses of pupae of *G. morsitans* from predators of this kind may be fairly considerable. Mongooses are particularly implicated. Lloyd found that on Riamugasire Island, from April to June 1933, 3·1% of 49,897 pupa-cases of *G. palpalis* and 1·0% of 879 cases of *G. brevipalpis* showed signs of destruction by insect predators. These are minimum percentages, as in numerous cases too little of the pupa was left for it to be possible to diagnose predator attack.

3.—ENEMIES OF THE ADULT FLIES.

(a) Insect predators which attack the flies on the wing.

The wasp *Bembex* and dragonflies definitely search animals and the backs of men for such flies as they may be carrying, and on Maboko Island, at first, with the tsetses very numerous on the screens of the traps, these were searched by great numbers of dragonflies, largely *Cacergates leucostictus*. The tsetse's reaction to this form of search is to disappear into the vegetation, and the dragonflies do not follow into close cover.

Temporary disappearance of tsetses from an area have been ascribed by the natives in the Lake Province to the appearance of vast numbers of robber-flies (ASILIDAE), which they call in Shinyanga "Simba ya sali" (the tsetse fly's lion). Robber-flies have been seen by ourselves preying on tsetse, but whether the vast numbers described actually do exterminate the tsetses and whether, if so, the effect is entirely direct or in part deprivative, by keeping the flies hiding in refuge-cover and by preventing them from feeding, we have had no opportunity to determine.

Stationary (lurking) predators that catch tsetses that are on the wing are the various web-making spiders. These are so incredibly abundant on some of the Sesse Islands that Fiske, after comparing the fly population of spider islands with others, considered that certain islands noted as very lightly or not infested might owe their freedom to the spiders. Carpenter also noted that in places "the sheets of webs may be seen in planes one behind another with scarcely a foot of space in between, and in such extraordinary numbers that the spiders on the central webs can scarcely get enough food. . . . An individual web may measure several feet, and be strong and sticky enough to entangle birds. The fact that abundance of spiders is correlated as a rule . . . with few *Glossina* has been mentioned already, and the question arises: Does predominance of the spider act as a check upon *Glossina*?" (Carpenter, 1919).

(b) Birds.

"During my first week at the Kanyezi vlei I was camped 150 yards or rather more from a considerable cluster of male flies. These were preyed on daily, sometimes continuously and for a long time, by half a dozen to eight birds belonging to three species—*Dicrurus afer* [= *Dicrurus adsimilis divaricatus*, the common drongo], *Bradornis* [*Melaenornis*] *ater* [Mimetic fly-catcher—now known as *M. pammelaina*] and *Bradornis pallidus murinus* [Mouse-coloured flycatcher]. From the continuous nature of the attacks, and the immense number of house-flies (*Musca domestica*) that tame drongos of my own have shown themselves capable of devouring in a very short time, there could be very little doubt that the birds were making considerable inroads into the male fly population, and it was likely that the practical disappearance sometimes of this cluster was in part due to them [through reduction or being driven to hide]. The birds perched on the low trees bordering the vlei and dropped to the tsetses in the grass below.

"In my general experiments I found that many birds [including rollers] disliked Muscid flies, including *Stomoxys* [*S. niger* and *S. calcitrans*], replete or empty (actual *Glossina* not tested), but that drongos, flycatchers, stonechats, swallows, bee-eaters, and some commoner small searching birds (*Turdoides*, *Phyllastrephus*, *Apalis*) liked them very much; drongos and swallows (certainly also flycatchers) continued to feed on them when so replete as to refuse all non-Dipterous insects. The digestion in at least two of these last three groups is so

rapid that (in my experiments) even when the birds were replete three or four minutes' rest [from feeding] made room for two or three or more flies. [Some of] these birds must be relatively formidable enemies to a fly the males of which display themselves so freely, and it is a pity that the population of such enemies must be limited by their dry-season food supply. Birds are in the habit of paying special attention to insects, otherwise acceptable, that are present in numbers together, so that in localities in which the flies are scattered they must lose a far smaller proportion of their population through the attacks of birds" (Swynnerton, 1921 : 368). Actually it has been rare to find *G. morsitans* in such conspicuous swarms in other localities, except when accompanying animals. The Yellow- and Red-Billed Ox-Peckers (*Buphagus africanus* and *B. erythrorhynchus caffer*) were stated by the natives in Portuguese East Africa to prey on tsetse on animals.

(c) Predators which search bark and crannies.

"The flies also no doubt continually come within the ken of the birds that carefully search tree-trunks and twigs, and it is in relation to these and perhaps to the spiders to be referred to that their choice of protective resting surfaces is likely to be of use. Such birds form a very large proportion indeed of our small bird population. Spiders of various bark-hunting species that hide in crannies and leap on their prey actually accounted for a number of the flies I had under observation in the net, and it is probable that these are the female tsetse's most important enemy" (*ibid.* : 368–69). I still hold this opinion. The spiders (SALTICIDAE) are sometimes very numerous, they react to the very smallest movement and the sudden leap of so small an object must be very much more difficult to forestall than the attack of a large-looming bird. Ants running about on tree-trunks probably keep the tsetses on the move rather than kill very many of them. Some details as to the bark-searching birds is given under heading 5 (pp. 233–235 below).

4.—INDIRECT EVIDENCE OF THE IMPORTANCE OF ENEMIES AND THE FEMALE TSETSE'S RESTING ADAPTATIONS IN PROBABLE RELATION TO THEM.

In an experiment on *G. morsitans*, *G. pallidipes* and *G. brevipalpis*, in which a very large mosquito net was erected over cut-back tree-trunks, shrubs, etc., and "furnished" with stems having different kinds of barks, stones, etc., it was noted, as quoted already in another connection, that the female tsetse especially possessed habits that were definitely procryptic. "The rough-barked stems were selected in preference to the smooth, and larger and small holes in the trunk and grooves in the bark were freely utilised for hiding in. . . . A distinct colour-harmonisation took place also, the blacker tsetses (*morsitans*) choosing blacker bark, the greyer grey bark, the brown ones (*brevipalpis*) brown bark and the underside of rough or knobby lianas, on which they easily passed as one of the knobs. . . . The excellence of their concealment was shown when I finally cleared the net. Both I and two smart natives searched every inch of its contents most thoroughly, as we thought, until we could not find another fly. I then passed my hand over the various surfaces and in this way flushed four more flies, all females, from the *Diplorhynchus* trunk. . . . The hiding flies were mostly, but by no means entirely, females. From my observations in the field also, it seemed clear that in *Glossina*, as in so many other animals, the female trusts mainly to concealment for defence against enemies, the male more largely to activity, and that the difference in the requirements of the

sexes and their methods of meeting them is the chief reason for the female's special seclusion, though Lamborn's factor (avoidance of males) may be operative also " (*ibid.* : 366–7).

The colour-adaptation here witnessed has probably a relation to those sharp-sighted enemies, birds, and to the jumping spiders, which obviously hunt by sight. If it were not for this colour-selection the habit of settling in grooves and holes might have been accounted for sufficiently as of use for the retention of moisture—a purpose it no doubt also serves. The colour-selection would constitute sheer hypertely as a protection from the male flies, which in any case are not bark searchers.

The fact that, when they are active, tsetses do not trouble to conceal themselves is due solely to the fact that they have now exchanged for concealment the defences of activity and alertness. This is paralleled fully by the case of the most palatable of butterflies (of numerous species) which when at rest trust to the harmonisation of the underside of the wings with the surfaces they select to rest on, but when feeding or laying eggs and therefore inevitably conspicuous, transfer their trust to activity.

The tendency of tsetses to disappear under attack by dragonflies and *Bembex*, mentioned above, is an exchange of the defence of activity for that of concealment. It is equally paralleled in the butterflies, the more palatable species of which simply dive into the herbage and stay there in face of persistent attack by a flock of bee-eaters, while the highly nauseous Danaines and Acraeas continue to sail about (Swynnerton, 1915 : vi). The habit of going to ground is therefore at least a suggestion of the probable palatability of the tsetses.

5.—THE INTENSITY OF THE ATTACK AND THE FACTORS WHICH WILL AFFECT IT.

(a) Closeness of search.

Only a field ornithologist who has observed long in Africa can realise how close is the search of twigs, tree-trunks, and thicket stems, of such birds as the yellow-streaked bulbul (*Phyllastrephus flavostriatus flavostriatus*), the round dozen species of bush-warblers of the genera *Apalis*, *Eremomela* and *Camaroptera*, the " white-eyes " (*Zosterops* spp.) and the wood hoopoes (*Phoeniculus*), and how necessary it must be for tsetses definitely lying-up to be well protected against them (*ibid.* : iii). Some of the bush-shrikes (*Laniarius*, *Tshagra*, and *Chlorophoneus*) also may well come into this category. Many other small birds search carefully the ground and the low twigs, but these come into contact with the loitering male rather than the hiding female and may not be too expert in catching him. Such are the helmet-shrikes (*Prionops* and *Sigmodus*), the ground-bulbuls (*Phyllastrephus terrestris*), the bush-robin (*Pogonocichla stellata*), the half-dozen robin-chats (*Cossypha*), some of the ground thrushes (*Turdus*),* the several scrub-robins (*Erythropygia*) and the babblers (*Turdoides*).

(b) Variation in the intensity of attack.

Actually, and especially as regards the predators that attack on the wing, intensity of attack varies immensely from week to week and even from hour to hour in relation to any species of prey, as I have for many years noted both directly and through the examination of, during that time, more than 1,000 bird stomachs.

* Remains of Diptera were found in the stomach of *Turdus olivaceus swynnertoni* Bannerman.

(i) *Variation through the relative abundance of the prey.*

It may be repeated that birds tend to concentrate on those species that, of their normal and preferred food, are at the moment most abundant and available. The persistent attacks on tsetses quoted above were indirectly due to the fact that the flies were forming conspicuous swarms on the grass which made it worth while to feed on them. On the other hand, as soon as a species becomes a little difficult to find in comparison with other and equally palatable species, the birds leave it for these. This fluctuation in intensity is less marked, though not absent, in the case of the bark-searching birds, which search the bark closely in any case. More probably, in the case of the ground scratchers, which, while not concentrating on grass-corms, they scratch for what they may find, and often scratch solely for grass-corms, or seek seeds, to fill up on, as a bee-eater fills up on bees.

It follows from the above that species which are commonly more abundant and easily captured than tsetses, but which are equally acceptable to the enemies of the latter, may be regarded as "buffers," protecting the tsetses from attack. Muscid and other flies, including gnats and hoverers, are commonly more available to drongos, flycatchers, swallows, and other eaters of Diptera than are tsetses; and swallows have been watched for long periods on the Huruhuru Plains sweeping to and fro between the animals in herds of cattle for the sake of the Muscids attending them, and on another occasion picking small insects off the grass, on which tsetses, if numerous, might have been sitting. The species that in numbers may act as buffers, or at least divide with the tsetses the brunt of the attack by the searchers of stems, are the numerous bark-resting moths with concealing coloration, ants, large and small, of several species, woodlice, beetles, cockroaches and earwigs, small myriapods, spiders and, in the damper surroundings that suit *G. brevipalpis* and *G. austeni*, even small worms, and protectively coloured grasshoppers and crickets, under the loose bits of bark and moss that the birds pull off.

(ii) *Variation through fluctuations in the density of the cover and in the numbers of the predators.*

The late dry season, when the thickets used by some tsetses are leafless and visibility is better, may be a time of difficulty for them in relation to enemies as well as through lowered humidity—which latter, in addition to killing more directly, may kill through making the flies come out and show themselves, or through making them more visible when resting. Towards the end of this period also the local bee-eaters and the local birds that search stems are reinforced (sometimes heavily) for some months by such immigrants as the European bee-eater and the willow warbler—the immigrants sometimes, as Moreau has noted, amounting to 50% of the whole. On the other hand, one would expect that at these times the jumping spiders, probably a very important enemy, would also suffer exceptionally through birds, if not through the physical conditions, so that the extra destruction of the tsetses by one set of enemies may be counterbalanced by a reduction in the other.

The habit of a great proportion of the insectivorous birds of carrying out "drives" for their prey in which several bird species participate—a flock of ground-bulbuls, babblers, or helmet-shrikes here, parties or pairs of bark-searchers a few yards off, and above them the drongos and flycatchers (*Batis, Tchitrea, Bradornis, Trochocercus*), alert for what the others may flush (Bates, 1863 : 334–6; Swynnerton, 1907 : 34, and 1915 : cx)—produces the

result that each piece of covert is searched with special intensity every few days.

Nothing is known of the night enemies of the tsetse—whether, for instance, the small mice that then search the stems, such as the grey African dormice (*Claviglis*) and the tree-mice (*Dendromys*), find and eat many, whether the tsetses remain sufficiently alert at night to escape them, and whether *G. brevipalpis*, which is active at night, is eaten by bats—and so on.

6.—INTERACTION BETWEEN THE ENEMIES, AND BETWEEN THE COMPETITORS, OF THE TSETSES.

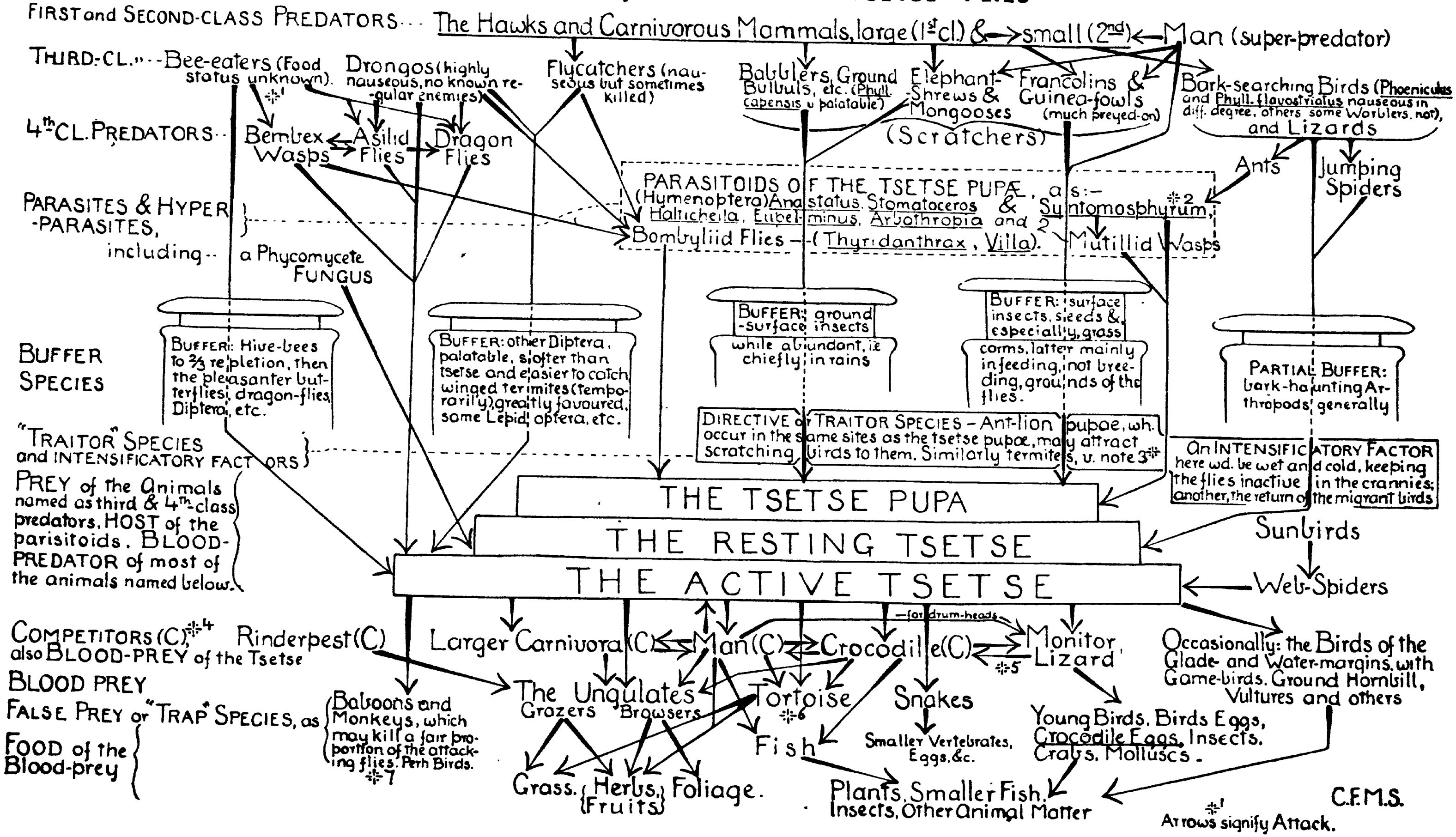
The parasitoid *Syntomosphyrum glossinae* attacks, as a hyper-parasite, the Mutillids that, like *Syntomosphyrum* itself, attack tsetse pupae. The latter parasite has been shown by our work on it to possess very deadly enemies in the form of some of the ants. Diptera-eating birds also eat freely the Bombyliid flies that are also parasites of the tsetse pupae. The bee-eaters eat dragonflies, the larger dragonflies eat the smaller, and the bark-searching birds will certainly eat the more palatable of the jumping spiders where they can, but the visits of the bee-eaters are mostly very passing, and the spiders are exceedingly active, while many of them are so brilliantly coloured above as to suggest that they may be distasteful. Wood-peckers for the most part hardly hunt low enough to be a serious enemy to the tsetses, and they probably assist the latter by eating great numbers of the bark-searching ants—but the latter still remain numerous. The bee-eaters and drongos probably eat *Bembex*, which has been seen to catch robber-flies and (very greatly) Bombyliids. The robber-flies have been seen to attack dragonflies. Again, some of the animals on which the tsetse feeds compete with it by destroying others of its food animals. This is well shown in table 40 below.

7.—EXAMINATION OF THE STOMACHS OF BIRDS.

Newstead and Davy in Nyasaland and Carpenter in Uganda carried out examinations of birds' stomachs in tsetse-infested areas. The former found tsetses in two stomachs out of 61 examined, representing 36 species. Considering the chances, the difficulty of identifying the smaller debris, the probability that " buffer " insects were present, and the fact that on the average less than two stomachs of each species were examined, and that many of the species were doubtless unlikely subjects, this was really not too bad a proportion. Carpenter (64 stomachs) was unsuccessful, but it must be remembered in each case that one could expect no result except from three groups—the Diptera-eaters, the bark-searchers and (for pupal remains) the ground-scratchers; nor even from the Diptera-eaters, of which Carpenter examined a number, except where the tsetses were so relatively abundant that the birds were likely to be devoting special attention to them. Llewellyn Lloyd examined ten guinea-fowl crops for pupae, and Newstead eight, without success. The numbers were too small, and these birds are in any case less likely to be formidable eaters of *G. morsitans* pupae than of those of the thicket-breeding tsetses; further, Newstead's birds were engrossed in eating corms, of a kind which in Shinyanga, at any rate, grow in the feeding-grounds of the fly, not in the breeding-grounds. My examinations of very large numbers of bird stomachs were not made in a tsetse area.

TABLE 40

THE "CHAIN OF ATTACK" OF THE TSETSE FLIES



Notes on the " chain of attack " of the tsetse flies, given in table 40.

*1. Arrows indicate direction of ATTACK, direct and (by man on the tsetse) indirect.

Even the browsing ungulates attack the tsetses indirectly when their numbers are uncontrolled (*see* fig. 19 on p. 281).

*2. *Syntomosphyrum*, as well as being a parasite of *Glossina*, is a hyper-parasite of *Mutilla*.

*3. The thickets which grow on and round large termite mounds are scratching-grounds of the guinea-fowls and, often, breeding-places of the tsetses.

*4. Destroyers of the food of the tsetses and so their competitors, as well as, in most cases, their prey.

*5. Monitor lizards feed on crocodile eggs, and the crocodile, when it can, on the monitor lizards.

*6. The remains of a tortoise were found in a crocodile by myself.

*7. That, however, tsetses often feed successfully on baboons was indicated by Johnson's and Lloyd's examinations of their gut contents.

8.—"PYRAMID OF NUMBERS" AND "FOOD-CHAIN."

While one can state the populations of tsetse, game animals, and large carnivora, in some of our "Blocks" at Shinyanga with a rough approximation to accuracy, and can estimate the percentage of pupae attacked by the various parasites, so little has been done towards the computation of the density of the predator-species which feed on the tsetses, that Elton's useful idea of the "pyramid of numbers" cannot yet be applied to these flies. Even without this, the ratio of game animals to tsetses would, if arrived at approximately in a number of different localities, enable us to check our view (*a*) that a very small food-population is as good as a large one for the feeding of blood-predators, and (*b*) that qualitative differences may be present as between different species of prey that tend to the production of larger or smaller populations of the tsetse flies.

Table 40 on p. 236, shown graphically but more simply in our museum at Shinyanga by means of actual specimens, illustrates how complicated are the relations between the animals that destroy the tsetse and those again on which the tsetse feeds. The arrows represent "attack on," not, as is more usual in "food-chain" tables, "entry into as food." The former was found more convenient for exhibition and enables us also to include man and the rinderpest. While man destroys tsetses (directly and indirectly) and crocodiles and monitor lizards, he does not, with the exception of one or more crocodile-eating tribes, feed on any of these.

9.—THE POSSIBILITY OF UTILISING THE ENEMIES OF THE TSETSES.

There are a dozen parasites which still might be tried, and some of which will probably be tried, but it is certain beforehand that, while parasites may reduce the tsetses greatly and be used as an auxiliary measure, they will not alone extinguish them, or even enable cattle to be kept, except under special conditions; for a very minute population of tsetses prevents cattle-keeping or makes it precarious. Further, in the case of an animal dependent on one species of prey, the last predator will die before the last individuals of the food species.

Protection will not help the vertebrate predators, for though man takes some toll of them he is by no means the chief of their enemies. The only real way to help them is probably by cover-control—the alteration of the environment by organised burning or no burning in such a way as to favour the more formidable enemies or competitors of the tsetses. The subject has, however, not yet been studied in this special connection. It is known already that the two alternative means of cover-control suggested will produce completely different bird populations, and that the bark- and twig-searchers are likely to be increased by not burning. The effect of any increase in such enemies will be merely contributory, not exterminative.

R.—BALANCE IN TSETSE FLY POPULATIONS.

No real work has been done on the problem of balance in tsetse fly populations, though Jackson proposes to take it up. In the meantime I propose to state some hypothetical and semi-hypothetical suggestions purely in the hope of attracting attention to the question.

In Block 4A, I have suggested that "the present balance has probably been attained mainly by a process we had observed elsewhere already under our measures of reduction and which in some tracts occurs seasonally also—close concentration of the survivors in only the most favourable spots—though the

converse of the factors that help to bring about balance at the high end of the density scale will have assisted. These (at the high end) may include the greater numbers of males that will assault each female when the population is great and so perhaps cause much abortion (Lamborn, 1915; Nash, 1930); special attention by birds and other enemies when it is worth their while (Swynnerton, 1921*b*); and in extreme cases the driving of the pestered game animals to live more in the open; also the converse of the factor first mentioned, namely, the greater diffusion of the fly population through good and less perfect habitats, that was notable in the great fly populations of Shinyanga when the writer first came there" (Swynnerton, 1934 : 419).

I feel from a modicum of actual observation that predators are probably much more important in relation to tsetse than is commonly supposed, when the tsetse population reaches numbers that make it worth their while to attack it. There is little evidence that disease (such as the Phycomycete fungus described earlier) takes an appreciable toll.

Further, some bloods are more favourable than others, and the flies may become specially attached to the favourable species if they are constantly present, and, if these animals are tolerant, may soar higher in numbers than when other species only are available.

Again, while a small game population may support a fair density of tsetse, game animals vary in their tolerance from (say) hartebeest, which are very intolerant, to buffalo and pig, which are very tolerant, and the desertion of a locality by the tolerant animals may lead to such a concentration of the local tsetses on the less tolerant species as will lead to desertion of the locality by the latter and consequently to a reduction in the numbers of the tsetse. This effect might be specially marked if the tolerant animals also supplied more favoured blood than the animals that remained. To this may be added the possibility (supported by slight observation) that individual tsetses accustomed to an animal species may not take quite readily to another; and in this is inherent the further possibility that the tsetses may, like birds, sally to the attack of a favoured species sooner, as regards stage of hunger, than they would attack a less favoured species, so that even with the latter present they may be feeding mostly on the other and be handicapped by slowness to adapt when the crisis comes.

Here may be added the view, referred to above and based on observations in the laboratory, but lately contradicted by Mellanby's results from *G. palpalis*, that excessive assault by males leads to abortion, and that, when fly density is high, every female that appears in the open is liable to heavier and more certain assault than when the numbers are low.

When I first went to Shinyanga, the position of *G. swynnertoni* was as given in the quotation above. In Kikore, during a considerable part of Nash's four years of observation, *G. morsitans* was spread in great numbers through several types of environment. A bad season, or a nearly successful measure on our part, suffices to drive the individuals of *G. swynnertoni* that survive it to concentrate on the hard-pan strips. A bad season in Kikore (1929–30) left *G. morsitans*, greatly reduced, in its most favourable habitat only. The very fact that the flies, through sheer density, had spread out into habitats only temporarily favourable and there had increased and multiplied, led to nemesis in the shape of a spectacular reduction of the population when an unfavourable season arrived. So that here also high numbers bring their own downfall, though an independent weather factor is the immediate cause.

Spread is apparently largely dependent on density, and it would seem that reduction by weather factors may depend to some extent on spread. Even if

one takes the seasons of a single year, the spread of the population in the rains and early dry season, following its annual increase, into areas that cannot support it in the annual drought, must, by the destruction of the outlying flies that fail to find fitting concentration sites, contribute materially to the great drop in true density that takes place near the end of each year.

A strong line is commonly drawn between what Jackson has called the "independent" limiting factors, such as climate, and the "dependent" factors that are brought into play incidentally to a rising population. In this case at least it would seem that the first are not wholly "independent." A cyclical effect, dependent on weather and spread, is also incipiently indicated; for the effect of favourable seasons (poor rains, ending early) has shown itself at Kikore in the rapid return of the fly population to its old and dangerous limits (and an approach to its old numbers in them) within three years after the catastrophe. The latter would in due time recur with a return of the weather-cycle, and the alternation would go on indefinitely, if it were not for the intervention of reclamation, now impending.

Within limits, however (Jackson suggests), the independent factors, *i.e.* those that do not necessarily depend for the intensity of their action on the density of the tsetse, can bring about marked fluctuation in the density before any of the ordinary "dependent" factors can come at all strongly into play. We see this happening every year. It is possible, of course, that the weather factors that are responsible for the tsetse's contracted distribution in the drought of the late dry season may often then cause crowding in excess of the optimum density, and so bring one or more of the "dependent" factors into play.

The "carrying capacity," as regards tsetse, of country that all seems suitable appears to vary enormously. In part small differences in the vegetation and vegetation-concurrence, and in part doubtless the food species and their habits, certainly contribute to this, but it is also very doubtful whether the flies in (say) South Tabora, fill all the places that they could if their population increased. There may be a social instinct which herds them into aggregations in a few of those places only; the way in which a fly advance holds together seems to support this view. But this leads us back to the question "What in that case is keeping the general population so much lower in Tabora than it is in Kikore that the flies are found in aggregations in the former locality and more evenly spread in the latter?" The whole question is of practical importance, for, if social instinct and not environment alone produces the concentrations that we see to-day in a few sites only, attack on these sites may merely produce a shifting of the fly population to an equally good site nearby.

Fly density will be determined by a number of factors, but it may well be determined in part by the presence, in varying extent, of country that is favourable to colonisation during a varying number of years, but which at intervals becomes temporarily unfavourable.

We can hardly say yet what the saturation point of tsetse density is for different types of country, but at Kikore (for *G. morsitans*) it must very nearly have been reached, as also at Shinyanga (for *G. swynnertoni*) in 1923, apart from the startling, localised, and probably very temporary, concentrations that one has found in more limited localities when the flies were "like bees." That the flies should readily reach large numbers under perfect vegetation conditions and with regular habits on the part of favoured and complacent food species till the natural checks bring them down is the perquisite of a blood-predator. To a blood-sucker a few dependable and otherwise favourable food animals are as good as whole herds, provided that they tolerate its attacks.

PART 3.—EXPERIMENTATION IN ATTACK.

A.—METHODS OF DIRECT ATTACK.

1.—EXPERIMENTAL BREEDING AND RELEASE OF THE PARASITE *SYNTOMOSPHYRUM GLOSSINAE*.

As it was found that this parasite could be bred by the many million with ease and very cheaply, it was felt to be worth persisting with even after initial failure. The experiment, initiated by Nash in Kikore, continued for four years, and the steps in it, being a record of one difficulty after another overcome, are worth recording, both for their interest and as an illustration of the delays inseparable from research work. The parasites were bred on meat-fly pupae in large, deep square wooden boxes with sand on the bottom and muslin covers on the top.

(a) Experiments at Kikore.

At first 79% of the meat-fly pupae remained unparasitised, but this figure was reduced to 6% by the better lighting of the cages. Then a mould destroyed the pupae, and the remedy proved to be better ventilation.

Again, a useless parasite (*Trichopria* sp.) of the meat-fly pupae regularly anticipated the *Syntomosphyrum* and threatened the experiment with failure. The remedy was found by an African laboratory assistant, named Yusufu Cheke, who spontaneously experimented in placing meat-fly pupae in boiling water and nevertheless obtained parasitisation by *Syntomosphyrum*. Closer work undertaken by Nash, who subjected meat-fly pupae to a series of different temperatures. Up to 49·5° C. no effect was produced and 95% of the pupae produced blowflies; 52° C. was the death point, no meat fly surviving to emerge at or above this temperature. Further investigation showed that a temperature of 50° C. was enough to sterilise the eggs of the undesired parasite, and was at the same time sufficient to reduce the vitality of the pupae to the extent that 1% or less of the blowflies now evaded *Syntomosphyrum* and emerged and 24% were dead. The remaining 75% of the pupae were successfully parasitised. The method has been incorporated in practice.

Such demands were made on the local blowflies that they became very scarce. The tins with the meat were then placed in new localities. Repeated attempts on the meat by driver ants (*Anomma*) and the larger carnivora also had to be frustrated. In general the technique so improved that whereas at first 23,000 blowfly pupae would only have produced 100,000 parasites, the same number at the end of a year's experimentation was yielding a million.

At first 100% of the parasitised blowfly pupae liberated in the breeding-sites of the tsetse fly were destroyed by mice and other predators. The mice were excluded by putting the pupae out in bamboo tubes with the ends stopped with clay and an emergence hole present. Still 75% were destroyed by other predators, chiefly ants. Smaller holes were bored, but the ants still forced an entry through the earthen plugs and white ants devoured the tubes. In October a large number of metal shaving-stick tins were obtained from England. Holes, 0·75 of a millimetre in diameter, were bored in the tins—large enough only for the parasite. Success was instantaneous; in September, 92% had been lost; in October only 4% were devoured. Between December 1930 and September

1931 only 1½ million parasites had successfully evaded the predators. Using the tins, in the month of December 1931, over 1¾ million emerged from one batch only and Nash found himself able to breed and release two million parasites monthly at a cost of 70*s.*

Unfortunately the view mentioned in my annual report for 1934 (p. 1) was confirmed, namely that the *Syntomosphyrum* is a poor burrower in soil containing little humus. Released in large numbers monthly on the escarpment north of Kikore, with its masses of rocks and breeding-places, it raised the parasitism rate of *G. morsitans* from 0·2 to 11%, but it failed to go further than this. The natural parasitism rate of 0·2 was calculated on 5,168 pupae examined during four and a half years.

(b) Experiments on Riamugasire Island.

The whole cause of failure at Kikore was apparently the insufficiency of humus. *G. palpalis* in localities on Lake Victoria breeds in almost pure humus, and, on investigating Riamugasire Island near Musoma, Nash found that the conditions were apparently perfect. Therefore, Lloyd, his successor in the experiment, was instructed to transfer it to Riamugasire and did so in March 1933. Despite every care, great numbers of these delicate parasites died on the long journey—160 miles by lorry, 474 miles by train, and 123 miles by lake steamer. The survivors were installed in Musoma.

Recovery was slow, the high monthly outputs of Kikore failed to be reached in Musoma, and Jackson, who was later in charge, found by experiment that under the conditions there the number of parasites per blowfly pupa required to be different (4 : 1) from the optimum number in Kikore (7 : 1). On the rectification being made, numbers again soared upward.

The humus bed all over the island was deep and unmixed with soil and the *palpalis* larvae were duly pupating in it. Nevertheless, the monthly results of the releases of the parasites in the field were more disappointing than even those of Kikore. In one month, for instance, in which 519,000 emerged on the island only 5% of the tsetse-fly pupae examined after the releases were found to have been parasitised.

On his return from leave, Lloyd was instructed to make a thorough investigation of the causes of the parasite's failure before the experiment was abandoned after so much work and so many difficulties overcome. He found first that minute ants, locally present, were able to get through the indispensable pin-holes into the tins, seizing the parasites as they emerged, and that the loss was probably in the neighbourhood of 100%. He proposed to allow all parasites to emerge in the laboratory and to release them after a feed of sugar-water.

In the preliminary experiments in the laboratory the parasites that were given sugar-water were found to develop a higher mortality rate than the unfed controls. In the experiments carried out at the same time on the degree of humidity that the parasites would support, it was found that an 85% rate was optimum and an approach to 100% fatal. It was surmised that the high mortality in the tubes supplied with sugar was due to the fact that the moisture supplied by the latter approximated actually to 100%. As Buxton has shown that it requires very little moisture in the soil to raise the humidity of the air contained between its particles to 100%, and as this was likely to come about even more readily in the interstices of a 2-inch layer of humus such as exists on Riamugasire, the possibility was visualised also that *Syntomosphyrum glossinae* would not succeed on Riamugasire owing to an excess of humidity in

the humus. Special experiments now in progress in Shinyanga are suggesting that this view is correct.

2.—AN ENTOMOPHAGOUS FUNGUS OF THE PHYCOMYCETE GROUP.

Work on an entomophagous fungus of the Phycomycete group had to be discontinued when the Research Botanist (J. D. Scott) was retrenched. Material for the cultivation of the fungus was supplied to Johannesburg, and it may be possible for us to test it ourselves on *G. palpalis* under high rainfall conditions. Even so, the hope of success is exceedingly small, for the fungus, which is common enough, appears to become deleterious to the flies only in particularly intensive wet weather.

3.—DISCUSSION OF THE POSSIBILITIES OF DIRECT BIOLOGICAL CONTROL.

Our object, unlike that of the agriculturist in relation to his pests, is in most places to exterminate, not merely to control. No natural enemy is likely to exterminate completely, but such an enemy might conceivably be useful for preceding, and shortening the incidence of, and so cheapening, some other measure. There are also a few instances, even with tsetse, in which mere drastic reduction is all that is needed—as where incursion of the tsetses from a highly infested centre into country hardly suited to them is what must be combated.

4.—HAND CATCHING OFF BAIT-SCREENS.

The hand-catching screen. Preferably T-shaped in cross-section (pl. 10, fig. 2), the hand-catching screen is made of hessian or other material, and is carried slung under a rod or bamboo on the shoulders of two small boys. These screens are far more attractive to female flies than are the boys themselves, and the latter catch the flies as they settle on the screens. A special experiment by Lloyd in which different colours were tested showed that dark grey screens were the most attractive, at least to *G. swynnertoni*.

The concentrating sites of *G. swynnertoni* in Block 5A, measuring 13 square miles (pl. 10, fig. 3), without clearings, were ascertained by Lloyd, and a catching-out experiment confined to these sites (for some of which see pl. 13) was carried out by him with 40 to 50 small boys for over a year, careful and continuous records being kept. Fig. 10 shows the effect on the flies in the block generally. The flies appeared at one time to have been brought down nearly to zero, and it is possible that the constant small reinforcement which was going on steadily all the time across the surrounding clearings may have contributed to the fact that the flies were not exterminated. The evidence showed, however, that a considerable proportion of the females continued to evade attack and would probably have done so indefinitely.

The addition of an extracted animal scent to the screens may improve matters considerably, but whether it will bring about final extermination is doubtful. It was interesting that the scarcer the flies became the more closely were they confined to the hard-pan strips which form their chief concentration grounds. This habit assures the meeting of the sexes up to almost the last fly.

Lloyd, in June 1933, also carried out an experiment on Riamugasire Island with a dark grey blanket screen, to test the attractiveness of the latter for *G. palpalis*, for comparison with the similar experiments already carried out on *G. morsitans*, *G. pallidipes*, and *G. swynnertoni*. With the use of the screen 2,450 flies were taken with a female percentage of 26·3. These

figures, however, include catches made when the fly numbers and the female percentage coming even to man were exceedingly high. As this condition was most exceptional the two days which came into this period are ignored for the present purpose. Taking the remaining days, we have a total catch of 1,619 flies on the screen round, the female percentage being 25·1; and 1,573 flies on the control round (natives only), the female percentage being 15·7. Female *G. palpalis* thus resembles the other species mentioned above in coming more freely to screens.

The effect of the screen in bringing out the old females was particularly marked, as is shown in the following table :—

Table 41.

Baits for *G. palpalis*. A cloth screen compared with man.

	Old females	Young females	Proportion of old to young females
Screen . .	120	287	1 : 2·2
Control . .	47	200	1 : 4·3

It would appear, once more, that man is not a favoured host of the old female flies.

Four catches with a screen and four control catches without were carried out against *G. brevipalpis* round the island by Lloyd in broad daylight; but only three flies came to the screen and one to the control. A catch was also carried out at dusk till it was too dark to see; the flies appeared in numbers, but there was time to take only 27, viz. 14 on the screens as against 13 by the catchers of the control. It did not seem that screens would be as useful here—even at dusk—as for other species of tsetse. Lloyd found that the individuals of *G. brevipalpis* entering his tent at night settled very freely on his silvered cinema screen and he based thereon a suggestion for a trap for this fly.

5.—THE TRAPS EVOLVED BY THE TSETSE RESEARCH DEPARTMENT, TANGANYIKA TERRITORY, AGAINST ADULT FLIES.

When I wrote my annual report for 1930, our trial of screen traps already showed promise. They were developed from the hand-catching screens (pl. 10, figs. 2 and 3), on the following principles :—

The screen, mainly of hessian, attracts the flies to itself. These on arrival tend in any case gradually to move upward on the screen. Experimentation showed that dark grey cloth was preferred to hessian and black felt or woollen cloth to the dark grey at close quarters. A broad strip of dark grey cloth was therefore sewn across the top third of the hessian screen. Along its top was sewn a narrow strip of black woollen or felt-like cloth. This arrangement encourages the flies in their upward tendency and on reaching the top they are already between the jaws of the tectiform "lobster-pot" entrance to the transparent wire-gauze catching-cage that runs the length of the trap (pl. 8, fig. 3) or is central (pl. 10, fig. 4). The next move takes them buzzing against the wire and through the slit into the cage. The colour arrangement is best shown in fig. 15.

The chief types now are as follows :

(a) The PS (Plain Screen) Trap.

In this trap (a simple development of the hand-catching screen) the screen hangs from the mouth of a long wire-gauze catching-cage which runs along its top. This is highly effective under certain conditions for *G. palpalis*, though the male proportion caught is too large, but it is useless for *G. morsitans* and practically useless for *G. swynnertoni.*

(b) The AS (Awning Screen) Trap (pl. 8, fig. 3, and pl. 10, fig. 4).

This was originally called the SS (simple screen), but it has been felt that if called by that name the trap might be confused with the PS (or plain screen) trap. The " A " refers to the narrow awning which, projecting from the bottom of the catching-cage along the whole length of each side and shading part of the screen, forms the feature which distinguishes it from the PS trap ((a), above). The AS trap has proved very effective for *G. pallidipes* and *G. palpalis* and catches very high percentages of females, but is useless for *G. morsitans* and *G. swynnertoni.* The ASC (concentration screen) trap (pl. 10, fig. 4) is the cheapest form of this trap, but may be a little less effective.

(c) The JS Trap.

In this (as in (a) above) there is no awning but a wire-gauze guard passes in from the bottom of the non-return cage, right along, towards the screen, to defeat the habit possessed by *G. morsitans* and *G. swynnertoni* of flying back at the last moment by the way they came. One form of this trap appears to offer some promise for *G. morsitans* and deserves to be worked at further.

(d) The JV Trap (pl. 7, fig. 2, right).

" The ' V ' represents a target of the shape of that of a Harris trap, which shape is undoubtedly excellent, but the flies do not enter the V as they do in the latter trap. It may be completely closed, or completely open on the top, or completely open on the top and at the ends. The sides are simply two screens which are hinged or otherwise joined at the bottom and lean outwards away from each other like a pair of slanting ' JS ' traps; or the trap may fold like a Harris trap—from the ends. Along the outside of the top of each side is slung a long catching-cage, or two, end to end, with the gauze guard of the ' JS ' trap, the dark strip already described preferably underlying this guard—on the hessian. This trap has caught *G. swynnertoni* moderately and *G. pallidipes* well " (Swynnerton, 1933 : 76).

(e) The SV Trap.

" This resembles the JV trap in shape, and differs from the Harris, as does the JV, in the fact that the flies do not pass through the target but climb up outside it to catching-cages placed on its shoulders. There is no guard, as in the JV, but from the bottom of the outer side of each catching-cage projects an awning which may be quite narrow. The target is simply two screens hinged at the bottom. The trap is good, but owing to the extra expense of the two catching-cages, it has not been used much " (Swynnerton, 1933 : 82).

(f) Revolving-drum Traps for *G. morsitans* and *G. swynnertoni* (pl. 7, fig. 3, and pl. 8, fig. 4).

These flies are particularly difficult to trap owing to their reluctance to pass a barrier even at a distance of two or three inches. On coming opposite the

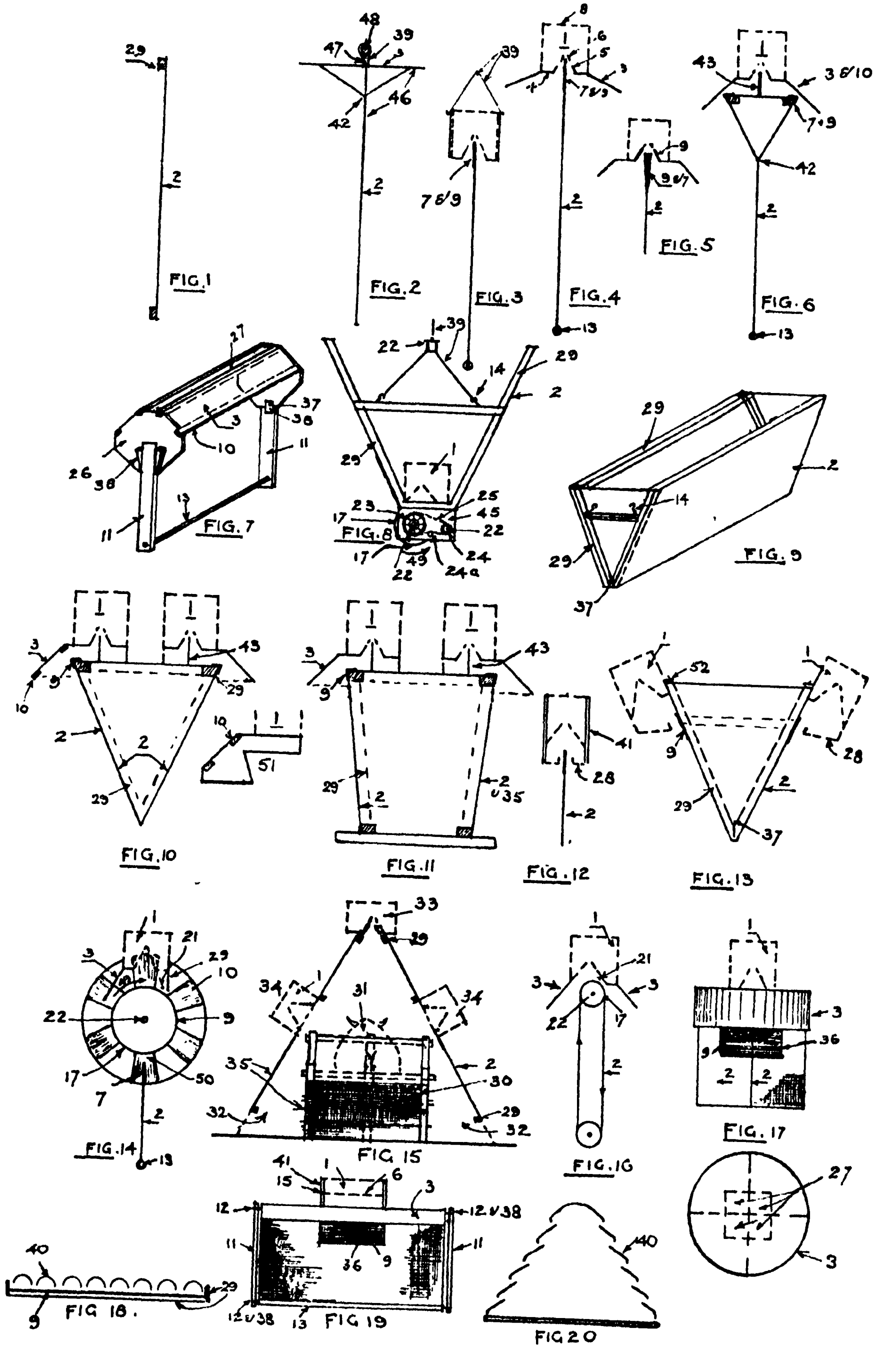


FIG. 13.—Details of various types of fly trap.

EXPLANATION OF FIG. 13.

Fig. 1, Cross section of the original catching-screen; 2, ditto of T-Screen; 3, ditto of PS (plain screen) trap; 4, ditto of SS (single-screen awning) trap; 5, ditto of Sy trap; 6, ditto of SY trap; 7, isometric view of the original wooden SSB (" buttock ") trap, ends made from petrol-box sides; 8, end elevation of the SVR trap; 9, isometric view of the target of the JV, SV and (except along bottom) SVR traps. Thickness of wood rather exaggerated; 10, cross section of SV trap; 11, ditto of SU trap (to contain an animal); 12, ditto of JS (Jackson's single-screen) trap; 13, ditto of JV (Jackson's V) trap, catching-cage shown unnecessarily large; 14, cross section of roller screen trap (SR) with fan shown behind; 15, DLA animal trap. The pen, shown too wide, came above the height of the calf and mosquito netting was swathed over the top; 16, cross section of BSR or Bax's " moving stair-case " trap, with the screen climbing round two rollers, one of which is supplied with a fan; 17, elevation or cross section and plan of the compartment trap (SCi); 18 and 20, rough plans of two forms of the Moggridge trap; 19, a concentrative screen trap.

In the various figures, no. 1 is the catching-cage or container, which may be covered completely with wire gauze or (fig. 3, nos. 3 and 12) have wooden or otherwise opaque sides; no. 2 is the screen, single, or (nos. 8, 9, 10, 11, 13 and 16 of fig. 3) double with space between; no. 3 is the awnings; no. 4 is the bottom of the container, from which rises no. 5, the non-return passage of convergent wire-gauze strips that form the entrance to the catching-cage, and no. 6 is the non-return aperture at or along their meeting-point through which the fly passes in; no. 8 is the top of the catching-cage, having a hinged or movable lid to it, which lid need not occupy the whole top or may be in the side or end; no. 7 is a board along the top of the screen to stiffen it; no. 9 is an attractant of black or dark cloth coinciding more or less with this board, or, it may be, covering the roller no. 17: below it or round it (fig. 1; fig. 3, nos. 17 and 19) may be cloth (no. 36) of some shade of grey, blue, brown or any colour that may be found to be the most suitable; no. 10 represents the supports to the awnings, whether attached to their sides, ends or both and whether of iron or wood; no. 11 shows two legs, which, passing down, serve as vertical stretchers to keep the screen stiff: they may be of any of several types (*e.g.*, fig. 1, or fig. 3, no. 7); no. 12 is the rings screwed in a vertical line into the catching-cage, and the ends of the horizontal stretcher at the bottom no. 13 (respectively) through which the legs pass; some alternative methods (no. 37 hinge, and no. 38 slot) of fastening the legs are shown in fig. 7 (in which the latter are shown too thick); no. 14 represents the screws, rings or hooks for hanging the trap; no. 16 is a hinge, bolt or screw at the junction of the supports of the awning and the lower corners of the container that enables these supports to be adjusted at will as to angle in the adjustable forms of trap: rigid supports for the awning, on the contrary, are shown in fig. 3, no. 7; no. 17 is the revolving roller or cylinder of the various roller traps, no. 18 is the wind-driven fan or propeller which makes it revolve; no. 20 is the brush to disturb the flies on the roller and make them fly up into the catching-cage; no. 21 is the trip-wire, just off the roller, which yet better dislodges the flies, though the " brush " or a board should still hang nearly to the roller to block the way out on that side; no. 22 represents ball-bearings; no. 23, in the form of gearing we are using at present, represents the large sprocket fastened on to the spindle of the roller; no. 24 the small sprocket attached to the spindle of the fan, and no. 25 the chain that connects them, while no. 45 is the block of wood, transferable from trap to trap, on which the whole gearing is mounted; no. 26 is the buttocks at the end of the SSB trap; no. 27 represents the openings into the catching-cage in the SSB and SC traps (fig. 3, nos. 7, 17); no. 28 is the gauze guard of the Jackson traps (figs. 12 and 13)—they and the catching-cages are shown unnecessarily large in fig. 13; no. 29 represents the wooden frame of a hand-catching screen and some other traps respectively; no. 30 is the calf pen inside the DLA trap; no. 31 is the calf, which, however, did not project above the pen, the top of which was closed with ordinary mosquito netting; no. 32 is the opening by which the flies enter the DLA trap; nos. 33 and 34 show alternative positions for catching-cages in the same trap—no. 34 was actually used; Hessian is indicated by no. 35 or coarse cross-hatching, grey cloth or its equivalent by no. 36 or horizontal hatching, hinges by no. 37, alternative methods of fastening the legs of the trap under no. 38, suspensory wire by no. 39, wire gauze in the Moggridge traps by no. 40 and petrol box (or wooden) catching-cages by no. 41; at no. 42 in fig. 3, nos. 2 and 6 or lower, the cloth forming the screen is drawn in—making in no. 2 an angle that is not too sharp for the entry of the catching-net; no. 43 is an extra board guide, with dark cloth covering, which, however, has not yet been proved to be necessary, and no. 44 is a tin of bird-lime to deter ants; no. 46 (in our present " T " hand-catching screens) is a frame of rod-iron, about $\frac{5}{16}$ inch, no. 47 the point at which the oblong dependant frame rivets (movably) on to the " T " or awning frame (also oblong) above it, and no. 48 the bamboo or other stick carried on the shoulders of boys from which the screen is suspended; no. 49 represents the direction in which a drum turns; no. 50 is a space between drum and screen to allow flies to pass, no. 51 the wooden ends of the catching-cages in the SV and SU traps, no. 52 the screws, rings or hooks for suspending the JV catching-cages from the " shoulders " of its screens.

bottom of the catching-cage during their ascent of the screen they almost invariably go down again. Eventually I tried a revolving drum covered with dark grey cloth and horizontally hung, which is turned by the wind and carries the flies that settle upon it round under the catching-cage, which hangs just above it. Arrived under it, they are tripped by a taut wire just clearing the drum, and, mostly, fly into the cage, perhaps at the third or fourth revolution if not at the first. The width of the entrance requires very careful adjustment, and it is found also that neither the awning nor the catching-cage should be less than 4½ inches from the drum. A tail vane and a bicycle hub or swivel, from the latter of which the trap is suspended, keep the trap head on to the wind.

Several patterns of this trap have come under trial (as pl. 7, fig. 4, and pl. 8, fig. 4) and it seems promising. An easy start and slow subsequent movement are necessary, and these desiderata have both been obtained amply by gearing, in regard to which Mr. Rosch has shown much ingenuity. The form of gearing now in use consists of bicycle sprockets and chains used in duplication (pl. 16, fig. 5). These can be obtained for nothing (except cost of transport) from old government bicycles, so that the whole cost of a large trap is about equal to that of a Harris trap. Our AS (SS) and PS traps, however, are very much cheaper, and it is hoped that it may be possible to get a trap as cheap for *G. morsitans* and *G. swynnertoni.*

(g) Manson's Electric Trap (pl. 8, fig. 1 ; and fig. 14).

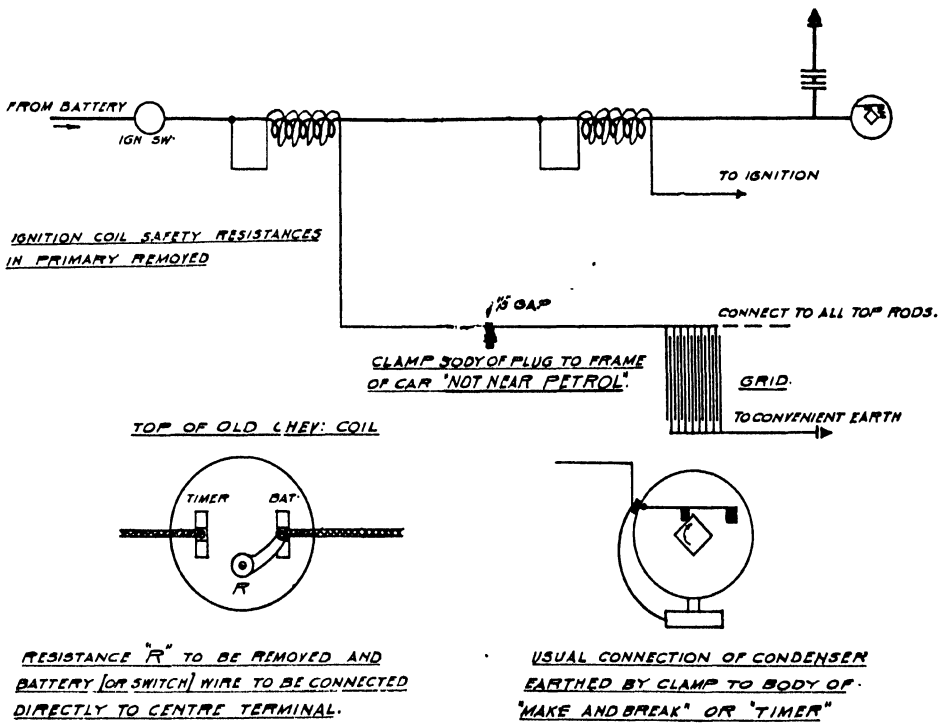


FIG. 14.—Scheme of the Electric Trap.

In response to a desire expressed by H.E. the Governor (Sir Stewart Symes) that the trains should be fitted with traps, I suggested a trap which was worked out in detail by Mr. H. Manson, Electrical Engineer to the Tanganyika Rail-

ways. This trap consists of a large oblong grid of thin iron rods, charged alternately negatively and positively, and backed with black felt for attractiveness. It fits the back of a lorry or of a guard's van and below it is fastened a tray containing a small quantity of a dense oil. Experiments in the workshop showed that voltages of 5,000 or 6,000, impracticable in practice, were needed to kill the flies, but that voltages of from 1,000 to 2,000 knocked them buzzing on their backs; hence the oil (suggested by Mr. W. J. McHardy). The trap was tried on the back of a lorry and the back of a train and accounted for nearly all the flies that settled on it. It becomes inoperative in wet weather owing to "shorting," and, as regards trains, can cover too small a surface to be fully effective; but it is otherwise an excellent trap and may find its uses.

Lorry traps on the "screen" principle have also been tried and have caught some hundreds of flies in single trips of a few miles, but a larger number of the flies always remains uncaught.

(h) Blunt's Land Sailing Trap.

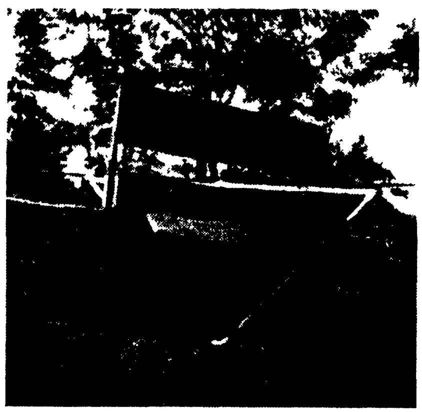


FIG. 15.—Commander Blunt's Sailing Trap. The bowsprit, partly shown only, is long and whippy and is turned, and turns the trap, on striking a glancing blow on an upright post at the end of each run.

The object was to obtain a trap that would move progressively and continuously: for progressive movement is highly attractive to tsetse flies. Blunt set to work and with his nautical instincts produced what is in essence a sailing-boat upside down. This trap was designed to sail to and fro on a wire and to tack automatically in a wind varying as much as eight points. To quote Blunt: "It is built on the same principle as the law governing sailing at sea, namely the triangle of forces brought about by the wind, the sails, and the resistance of the sea acting at right angles to the keel. At this point the resemblance has ceased, for the trap is borne on a wire instead of the sea, and the passengers, nearly all ladies, come on board by air when the ship is already under way."

A strong wire is stretched between two convenient trees across the prevailing wind. On this, run two wheel-pulleys, preferably with ball bearings. From these pulleys depends a triangular frame of light wood—isosceles or right-angled, with the hypotenuse upward. Pivoted in this frame from a bicycle

hub dependent from the middle of the hypotenuse is the " mast " or pivot-rod, on which is carried the sail, the fore portion of which, corresponding to a foresail, is in this case larger in area than is the after portion. The lower end of the pivot rod is carried in an open wooden bearing pivoting in the down-pointing apex of the frame. The sail is the screen of an ordinary AS or PS trap, with its colour attractants, narrowed at the bottom, and carried above it, in the same plane as itself, are the catching-cage, awnings, etc.

The sail is kept at the proper angle to the wind by two arms projecting from the top corners of the frame, these arms acting as " sheets." The wind, acting on the sail, which is kept at an angle to it by one of these sheets at a time, impels the trap along the wire. When it nears the end of its run, a bowsprit of springy wood strikes with a glancing blow a post placed in the ground to windward and a few feet short of the tree. The fore end of the sail, attached to the bowsprit, is detained by the post while the trap travels on and is slowed by the sail being brought up into the wind. This final movement of the trap before stopping turns the foresail sufficiently to bring the wind on the other side of the sail. The trap thereupon moves back to its starting-point on the other tack and is there put about by the same method. A narrow stretch of hessian is rigged above the cage in order to keep the trap on an even keel. If suitable brackets that can be passed could be made to support the wire at intervals, there is no reason why this trap should not travel considerable distances.

(i) Water Sailing Trap.

It is thought that Blunt's sailing trap might perhaps be worth trying in a modified form in shoal waters for catching food-hunting *G. palpalis* off lake-shore and islands. The hull, he suggests, should be completely turtle-decked in, thereby providing little or no free-board for the flies to settle on, and the catching-cage and screen, which would again be the sail, would pivot on the mast.

(j) Blunt's Spinnaker Trap.

The spinnaker trap is probably less useful than the sailing trap but is described below in case its details may give ideas to other experimenters. It is practically the same in construction as the original sailing trap, and is the complement of it, as its sail is set to move it in a following wind. The difference in the build of the trap lies in the longer rod, which holds the sail at the best angle for a following wind; and a catch to hold the sail fore and aft on its return up wind. The bowsprit is set at a different angle. The overhead wire in the spinnaker trap is rigged in line with the prevailing wind, while the wire for the sailing trap is at right angles to the wind. The trap has a strong cord attached to its after end which is led through a pulley, up and through another pulley (secured to a branch of a tree above the end of the overhead wire), and from its end is suspended a weight.

In a calm, the weight holds the trap to windward. When the wind blows, the trap is blown to leeward, thereby raising the weight. When the trap reaches the end of its run, the bowsprit strikes a pole placed upright in the ground, and this swings the sail round till it slips into a catch, holding the sail in line with the wire. There being no wind resistance by the sail, the weight exerts a pull and draws the trap back up to windward, where its bowsprit strikes another pole, and throws the sail out at right angles to the wind, when the trap will run before the wind, hoisting the weight again, and so on indefinitely.

In the above arrangement the travel of the trap is limited to the height that the weight can be lifted, but if the rope holding the weight is rove through a double and single block and the weight made fast to the double block, then the trap will travel four times the distance that the weight travels.

Another and possibly better alternative might be to connect two traps on overhead wires by a rope and pulleys, so that one trap when running free pulls the other trap to windward, when, both reaching the end of their run, they get their sails reversed and the trap to windward then runs before the wind, pulling the other one up to windward and so on.

(k) The Cavern Trap.

The cavern trap, a slight adaptation by us of Mr. C. W. Chorley's excellent crinoline trap, has been described in a paper (1933) by himself and is illustrated in pl. 8, fig. 1. Used by us against *G. palpalis* it gave good initial catches, but subsequently it was less successful.

(l) Scent traps baited with a live animal.

At first a calf was used in a tent-shaped (DLA) trap, so arranged that the animal was completely invisible (pl. 9, fig. 4). The catching-cages were in the sides of the tent. It was set in a space measuring 27 yards by 20, traps, Harris and SS (AS), set in which had caught from 30 to 100 flies *per diem* previously. Yet the calf trap produced a catch of 584 flies, of which 500 were *G. pallidipes*, in the space of $5\frac{3}{4}$ hours. The control trap, exactly similar but without a calf, was unfortunately only 4 yards away and got much of the wind of the calf. It caught 244 flies. Subsequent experiments with this and another kind of calf-trap (our SU trap, pl. 8, fig. 2) showed a continued strong disparity in catch between calf and control in favour of the calf, while nine experiments with the calf-trap, and control, with no calf in the former, showed an aggregate result that was slightly in favour of the control. It was not finally settled whether the flies were attracted from some distance away by the scent (as seemed most probable), or, having already arrived at the trap, were incited by the scent to greater persistence and so entered in larger numbers.

TABLE 42.

Catches of tsetse (*G. pallidipes* and *G. palpalis*) in feeding-ground 2 at Shinyanga on 18th September, 1932.

	Totals.	
Calf-trap in $5\frac{3}{4}$ hours . . .	584 flies.	
Control ,, . . .	244 ,,	
AS trap in the day	97 ,,	Maximum in this spot on any other day 62.
JS ,, ,, ...	31 ,,	,, ,, ,, 8.
Harris trap in the day . . .	97 ,,	,, ,, ,, 52.
JV ,, ,, . . .	58 ,,	But previous day took 99.

(m) Scent traps baited with animal extracts and chemical scents.

Whether the traps were baited with animal extracts or chemical scents, it was quite certain that the addition of an attractive scent to our traps would greatly increase the catch, and experiments were begun with a view to discovering how to produce one. Mr. C. B. Symes, collaborating in Kenya, made extracts with alcohol and ether from the testicles of a bull (following an observation by Napier-Bax) and the skin (sebaceous glands) of an ox. We tried them together on the experimental island Maboko. In the three traps used they were immediately successful in doubling and trebling the

catch of the traps in the catching-cages in which they were placed (in short test tubes), and the high catches continued for some days till the extracts deteriorated. This line of work is to be continued. The extended success of trapping depends undoubtedly on the extent to which we can develop scent bait, and the latter may prove of use (as Dr. Maclean has suggested in conversation) for mosquitos, *Simulium*, etc. Further it may render the cheapest forms of trap (such as the PS and Crinoline) attractive to a larger number of species of tsetse than they attract at present.

6.—THE TRAPS DEVISED BY THE TSETSE RESEARCH DEPARTMENT, TANGANYIKA TERRITORY, FOR THE COLLECTION AND DESTRUCTION OF PUPAE.

Noting that natural fallen logs in country with numerous rock-sites sheltered more pupae than the latter, Nash and C. A. H. Heard set to work and evolved the following trap (pl. 10, fig. 1). A tree-trunk eleven or twelve feet long is felled and placed on two rollers made of its branches. The ground is cleared just round it and pieces of bark stand up against its sides to darken the space underneath it. Every three weeks (or slightly less) native assistants go round the traps and roll each log a short distance along its rollers. The heat of the sun in the ground thus exposed (Nash found) kills any pupae that may have been deposited there as soon as the earth reaches a temperature of 112° F.

Each trap costs only 25 cents of a shilling to make; or five where a log fallen already is used. " During the two months (six traps) that followed the rains they gave a total yield of 477 deposits. This yield was exceedingly high, giving each trap an average deposit of 1·3 pupae a day in an area where fly density for the same period was only 1·6 per fly boy per 100 yards, or approximately 11 tsetse to a catcher in nearly half a mile." Nash, therefore, argues that if these traps averaged only one pupa apiece each day, thirty shillings worth—less than the price of one Harris or roller trap—would catch 120 a day, 3,600 a month or 43,200 a year. To which must be added the cost of the fortnightly visit. This would be necessary in the case of the other traps also and these, in addition, would need repairs and re-covering.

The method, tried at Shinyanga, was not a success against *G. swynnertoni*, but is being given a continued trial now at Kikore by Findlay against *G. morsitans*.

C. W. Chorley, in Uganda, has been experimenting with "Carpenter" pupa traps in the form of thatched shelters, to which however he has added catching-cages in the top to secure the mature females also. The result (against *G. palpalis*) he reports to be promising. That such a trap really well placed will take large numbers of pupae is shown by the following figures for one of the best catchers amongst Carpenter's own traps.

TABLE 43.

Catches by a Carpenter trap for the pupae of *G. palpalis*.*

Month	Pupae	Month	Pupae	Month	Pupae
1921		April . . .	877	May . . .	346
March . .	736	July . . .	711	August . .	679
June . . .	662	October . .	514	November . .	669
September . .	896	1922		1923	
December . .	79	January . .	211	February . .	64

* From Carpenter.

We have ourselves constructed a hollow log-trap of hessian to intercept both pupae and females. This has not yet been tried in the field.

7.—THE HARRIS TRAP (pl. 7, fig. 2, left).

In March 1931 R. H. T. P. Harris very kindly motored me from Durban to the Mfolozi Reserve in Zululand and showed me his traps at work (Harris, 1930*b*). Our own screen traps were already at that time in experimental use at Shinyanga. Their principle has been described on p. 245. That of the Harris trap is very different. In this, as in the crinoline traps (see below and pl. 9), the flies, which tend to go first to the belly, find there an opening into a darkish chamber and are attracted upwards to the light shining through the catching-cage in the roof.

Set in the places which here we regarded as feeding-grounds, the six traps seen at work appeared at the time of my visit to be catching from 100 to 200 flies each *per diem.* The largest catch had been 3,998 flies by one trap in twenty days, and the largest by one trap in one day 541; 75 traps in one month had caught 157,074 flies. The female percentage out of 340,000 flies caught was 80·5.

Since the visit referred to, large maxima may have been attained and definitely an enormous total has been reached. The latest figures are unfortunately not available to me at the moment.

The above early figures are given nevertheless to show what a really good trap can do against *G. pallidipes* under the good conditions represented by a large and concentrated fly population, a concentrated game population, and (it might be added for the first year) drought, which has a strong effect, at any rate in Shinyanga. There can be no doubt that Harris's has been a very fine achievement. I am doubtful whether complete and final extermination of *G. pallidipes* will be brought about by traps only even under the conditions of concentration obtaining in Zululand, but this species should at least be so very severely reduced there as to cease to wander out over the farms and native reserves to an appreciable or dangerous extent—and that will suffice to solve the peculiar Zululand problem.

Mr. Harris kindly gave me permission to experiment with two or three of his traps.* Actually two were used, and experiments were carried out against *G. morsitans* and *G. swynnertoni.* The Harris trap is capable of catching *G. morsitans* in considerable numbers under conditions of intense evaporation towards the close of the dry season, but numerous flies present do not enter and the trap is not regarded as likely to be useful for the extermination of this fly. Nor are our own traps likely to exterminate it. Against *G. swynnertoni* the Harris trap has been quite unsuccessful. Against *G. pallidipes* it is quite excellent in Tanganyika, as in Zululand; but in a nine days' fair competitive trial between it and our AS trap near Shinyanga the latter had rather the better of it. In a trial during the rains the Harris trap appeared rather the better, but the flies (*G. pallidipes*) were not coming appreciably to any traps, with the result that the numbers were too small to be worth much. Probably over a prolonged period under our conditions there would be little to choose between the two traps, but we are using our own as it is a good deal cheaper to make.

Against *G. palpalis* the Harris trap should be, and probably is, very good, but here, in a brief trial, our AS (SS) trap had the advantage in a marked degree. For this reason, and especially again owing to its cheapness, we are continuing to use it as our standard trap for this fly.

* Since the above was written, the patent rights in the "Harris Trap" in all parts of the British Commonwealth, other than the Union of South Africa, have been presented by Mr. Harris to His Majesty's Government in the United Kingdom.

The following tables give the results of two 9-day comparative trials between three different traps of the same length and depth, hung end to end a yard or two apart :—

TABLE 44.

A nine-days' trial, between traps of different types, in feeding-ground 1, beside Block 10c, Shinyanga, 2nd September (noon)–11th September (noon), 1931 (pl. 7, fig. 2).

(Averages *per diem.*)

	G. pallidipes	*G. swynnertoni*	Female % *G. pallidipes*
Harris trap	9·88	1·33	69·66
JV trap	6·58	3·20	67·85
Harris and JV traps combined	16·46	4·53	68·96
SS (AS) trap . . .	16·26	0·93	71·13
SY trap	15·24	7·22	76·08

In this trial the JV (Jackson's trap) catching-cages were mounted on the shoulders of the Harris trap. Each doubtless stole from the other, so they are shown combined as well as separately. Some of the figures were mistyped or otherwise altered in the version of this table as originally published (Swynnerton, 1933 : 77).

TABLE 45.

A nine-days' trial, between traps of different types, in feeding-ground 2, Block 9, Shinyanga, 15th–23rd September, 1931.

(Averages *per diem.*)

	G. pallidipes	*G. swynnertoni*	Average daily total, both species	Female % *G. pallidipes*
Harris trap .	39·62 (41·00 approx.)	0·37	41·00	58·67
JV trap . .	32·37 (38·82)	3·75	43·00	76·06
SS (AS) trap .	49·28 (50·98 approx.)	2·71	54·00	76·52

" In this experiment the Harris and the JV traps were separate. The detailed figures for all traps were lost for the 16th September, and for the SS for the 19th, so that the unbracketed figures of the first two columns and the female percentages are based on eight days and, for the SS (AS), seven days. Fortunately the totals have been preserved (and the ' both species ' column above is based on them), as has the fact that on every day in this experiment *G. swynnertoni* was caught in negligible quantities. If we should assume, then, that the same proportion of the latter species was caught on the missing days as on the rest the average total catches *per diem* of *G. pallidipes* would be as shown in the brackets. The SY trap was not used" (Swynnerton, 1933 : 77).

The AS against *G. palpalis.* A 6-ft. AS with awnings barely below the horizontal and without buttocks, was tried in May for 3½ days against a 6-ft. Harris trap on the Kuja River in South Kavirondo. Again the traps were end

to end, two yards from each other, each equally conspicuous on a high spit projecting into the flooded river. The results were as follows :—

TABLE 46.

The relative effectiveness of the SS (AS) trap and the Harris trap against *G. palpalis*.

	SS (AS) trap	Harris trap
17th May	30 *G. palpalis*	3 *G. palpalis* and 1 ♀ *G. brevipalpis*
18th „	54 „	7 „
19–20th May . . .	78 „	4 „
Total number of females .	118	12

". . . The experiments on the Kuja River have been continued by Mr. Symes on carefully controlled lines, and he writes to me two and a half months after their initiation that the screen traps still keep up their very strong lead" (Swynnerton, 1935 : 82).

It is believed that, given the same conditions as regards population of *G. pallidipes* as are enjoyed by the Harris trap (*see* p. 253 above), the screen trap might just possibly make equally spectacular catches. Our populations of *G. pallidipes* have been small. On the other hand, conditions (as of humidity) may make a difference as to the type of trap that will succeed.

8.—THE CHORLEY TRAPS (pl. 9, figs. 1, 2, and 3).

C. W. Chorley has done much work in the invention of traps for the capture of *G. palpalis*, and has been engaged on an experiment for the trapping-out of the species on Nsadzi Island, opposite Entebbe.

His traps for the adult tsetses are constructed on the principle of the " crinoline trap," invented by Richmond and Mendis for mosquitos in India. Imagine a sack held open like a lady's crinoline, by stiff wire rings, and a jar with a non-return entrance or a wood-and-wire catching-cage instead of the lady's waist, and you have a form of the crinoline trap. Its skirt can be wide or narrow; actually most of the traps used by Chorley are more like a loose trouser leg in width. He has had much success against *G. palpalis* with these traps, which have been described and illustrated more fully by himself (Chorley, 1933). Two, which he lent to me (and which he himself set on Maboko Island), caught large numbers of flies initially. These are the cheapest of all tsetse traps, but they need a close knowledge and experience of the fly in order to produce the success which Chorley obtains. So far as is known the narrower traps catch only *G. palpalis*; experiments of my own with the usual small Chorley traps against *G. pallidipes* were not successful. A very large trap, exactly equivalent to the original crinoline trap, was more promising.

9.—WILD ANIMALS AS AN AID TO CONTROL.

R. H. T. P. Harris, in his large-scale trapping operations in Zululand, reached (among others) the conclusion " that the presence of animals amongst fly traps is of great advantage in increasing the capture of flies." He recommends concentrating the animals in the area to be trapped by shooting them elsewhere—on the view that the game animals will bring in the flies from outside.

I fully agree as to the contribution which a game population can make to

successful trapping. I suspect, however, from results obtained for *G. pallidipes* at Shinyanga that scent may come more into the picture than has as yet been suspected; it is true that the flies tend to concentrate where the game concentrates, but the frequent presence of game near sight-traps will, through its scent, cause them to catch very much better and the concentration of game in the neighbourhood of Harris's traps might have operated, partly, thus. The question of the senses by which flies find their food has been debated already on pp. 203–206 above. In the case of *G. palpalis* on Maboko Island there appeared to be a connection between catch and the presence of animals: a trap was catching very badly, but one day during one of my visits a monitor lizard lay close to it in grass in which it should have been fairly concealed; up went the catch to a hundred. A similar instance has been reported more lately by Milambo. In this case a monitor lizard actually forced its way into the catching-cage of a trap that was catching nothing, and about 50 flies were at once captured. A landing-place that was much frequented by our natives for drawing water and washing became the scene of a very strong daily concentration of flies. A trap set beside it, starting with small catches, made in the end very large catches daily. The flies were certainly not carried to this spot by man to any great extent, for almost all human movement was *across* the narrow fly-infested shore strip and an occasional boat came in not coasting but straight off the lake. Animals were not present at all. Visibility around was poor owing to dense vegetation, and I cannot account for the concentration except on the hypothesis that the scent of man was the main attraction.

The manner in which the catches of fly rose when an invisible calf was placed in a trap (*G. pallidipes*), when cattle were passing a trap (*G. pallidipes*, repeated for *G. palpalis* in Maboko), and where scents extracted from animal glands were placed in traps (*G. palpalis*), has been described elsewhere in this paper. That the flies detecting an attractive scent do not easily detect its source, but go to the first conspicuous object detected, has been supported also by some of our observations. Such probable cases were those already referred to when cattle were in proximity to traps, those in which grey screens carried with cattle have done most of the catching, and cases in which, with game standing close by, the flies have come unusually strongly to ourselves. Moggridge on 10th November, 1931, with cattle herded near traps, caught four times the number of *G. pallidipes* as he did with the same traps without cattle: and the female percentage was 95·5.

Whether the above view is correct or not, there can be little doubt that attack with traps or by hand-catching in the feeding-grounds of the fly will be greatly assisted by regular and undisturbed habits on the part of large numbers of game during the greater part of the campaign and especially by a game concentration. Whether it will be useful (or sufficiently practicable) to drive the game out locally and temporarily at the end, when the last few flies are proving hard to exterminate and need special hunger to make them appear in full numbers, can be found out only from experience.

10.—EXPERIMENTAL ATTACK ON *G. PALLIDIPES* IN BLOCK 10C, IN SHINYANGA, WITH THE AS(SS) TRAP DESIGNED BY THE TSETSE RESEARCH DEPARTMENT, TANGANYIKA TERRITORY.

The following account has been condensed from the annual report of the Senior Entomologist, Mr. W. H. Potts, for 1932. This block appears to contain, for part of the year at least, more *G. pallidipes* than most of the bush

round Shinyanga. Even so they are not at all numerous, and are vastly less so there than *G. swynnertoni*. The block was partly separated from the surrounding fly bush by clearings in 1931–32. Money has not sufficed as yet either to isolate it or trap it at all completely, but the *pallidipes* population of the Ngongho strip had not recovered late in 1934 from the reductions made in it by the experiment to be described. The trapping was carried out by means of our screen traps of the SS (or AS) and ASB forms. These catch *G. pallidipes* well, but not *G. swynnertoni*.

Towards the end of August 1932, an experiment in trapping was started in the north of Block 10c—near the Ngongho only. By 8th October, a hundred traps had been put out in a fairly limited area in the neighbourhood of this river—a small, purely seasonal stream with thickets. The results discussed below are based on the figures from those traps obtained between 25th August and 29th November.

The traps were placed in sites chosen to test as far as possible the various factors which might possibly influence successful trapping of the fly. At first, when the traps were few, they were cleared every two or three days; but later, when their numbers increased, every week, the flies being killed with "Flit." A total of 17,162 flies were caught in the traps during the period under consideration. Of these, the majority were *G. pallidipes*, the percentage of *G. swynnertoni* in a week's catch varying from 5% to about 15% and generally being nearer the former figure. The female percentage of *G. pallidipes* varied from 72% to 83%. The analysis of the catches revealed a general and steady decrease in the numbers of flies caught from the outset of the experiment, and threw light on the factors which conduce to the successful siting of traps.

(a) Comparison of the behaviour of old traps in new sites with that of new traps in old sites.

A general decrease in catch was exhibited by traps in their original sites, and on removal to new sites, out of 14 traps, 8 showed a substantial increase, 4 little or no change, and 2 only a decrease; but the catches in the new sites never attained the magnitude of some of the earlier catches. In only one instance out of ten was there even a slight rise when a new trap was placed in an old site; in the other nine there was either a further decrease, or little or no change. It appears to follow that the application of "Flit" to the traps was not in itself responsible for the general decrease in catch.

It is suggested that the decrease in numbers may have been due

(α) to a general decrease in fly numbers (see above);
(β) to a certain degree of exhaustion of the old sites by the traps, as evidenced by the increased figures obtained in some of the new sites.

There is also a suggestion in the summarised figures that substantial decreases were *subsequent* to a short spell of exceptional drought, but this was not universally exhibited and the connection between the two phenomena needed confirmation.

(b) Analysis of the factors conducive to the successful siting of traps.

The relative success of 97 trap sites over a period of 6 weeks during October and November 1932 was compared in respect of the factors discussed below :—

(i) Heavy thicket is inimical; so is heavy overhead shade.
(ii) Light thicket, appearing unfavourable, proved to be only so when

combined with heavy overhead shade. There was only one exception to this in eight sites.

(iii) Glades and small open spaces in thicket, and thicket margins, are on the whole favourable. Of 40 such sites three only were ranked as unsuccessful, of which one showed the unfavourable feature of heavy overhead shade.

(iv) Mbuga (open seasonal swamp) was neither definitely successful nor unsuccessful, the number of successful and unsuccessful sites being equal on either side of a great preponderance of moderately successful sites.

(v) Close proximity to well-marked paths is possibly an advantage; of the traps near paths 9% were definitely unsuccessful as opposed to 19% of the traps away from them. Omitting the moderately successful traps 36% of the traps near paths were successful, as opposed to 11% only of those away from paths.

(vi) Proximity to a dry but enthicketed river and its tributaries seems to give a tendency towards success. Of the 56 such sites used 36% were in the successful class, as opposed to 19% of the 41 traps away from the river and its tributaries.

(vii) Sites in which the long axis of the traps (AS (SS), awning screen traps) lay east and west were more successful than not. Of 38 sites 5 only were unsuccessful and 4 of these could be accounted for otherwise. Traps lying otherwise than as above might or might not be successful.

(viii) Somewhat distant visibility appeared (curiously) to exert no influence whatever. This is doubtless related to the fact that thicket margins and to a less extent light thickets, conditions which imply restriction of visibility, are advantageous, while mbuga conditions, implying good visibility, afford only mediocre success.

11.—GENERAL NOTES ON TRAPS AND DISCUSSION OF THE POSSIBILITIES OF TRAPPING.

(a) General notes.

All the present traps may be improved by being made to revolve. This can be effected by hanging them from a bicycle hub and placing petrol tins diagonally bisected at each end of a screen trap, or, in a crinoline trap, at the four ends of a cross made with laths (pl. 9, fig. 1), this being Chorley's invention. Blunt has produced the same effect in a screen trap very ingeniously by twisting its lower margin into the form of an S; with any breeze at all it revolves continuously.

The Tsetse Research Department's traps for the adult flies, except Blunt's, have been more fully described in a paper by myself (Swynnerton, 1933), the log traps in a paper by Nash (1933*a* : 107–195), and Chorley's traps (1933 : 315–318) by himself.

(b) Discussion of the possibilities of trapping.

As regards the three species of tsetse of the *morsitans* group we find that it is only from July or August to October and at other times of the year when drought conditions produce strongly reduced humidity and therefore thirst-hunger, that they come to the traps in substantial numbers. *G. palpalis* comes strongly either in very wet weather (as Mr. Chorley has found in Uganda and we found on Maboko), or in a very dry spell such as happened on Maboko Island in January 1933.

"The following figures, collected by Dr. Jackson at Masiliwa from two

standing catches by boys without screens of ten minutes each daily for 51 days in the same spot, illustrate the general correlation between high evaporation and a raised catch of females. Livingston atmometers with white cups were used to measure the evaporation" (Swynnerton, 1933 : 96).

TABLE 47.

Correlation between high evaporation and raised catch of females at man.

Evaporation (uncorrected but intercomparable)	0–20 c.c.	21–40 c.c.	41–60 c.c.	61–80 c.c.	81–100 c.c.
Number of females captured daily in ten minutes	2·1	1·6	3·3	5·7	9·6

The rule applies also to captures in traps. When the evaporation rate exceeds 60 c.c. trapping becomes productive. In October (if rains have begun), or in November, the numbers fall off and during the rains tend to become negligible here even for *G. pallidipes*.

The following are some monthly means (corrected) for evaporation at Old Shinyanga :—

TABLE 48.

Evaporation rate at Old Shinyanga (monthly means).

	1931.	1932.
	c.c.	c.c.
January	—	54
February	38	34
March	28	28
April	26	24
May	45	39
June	53	54
July	58	—
August	70	—
September	72	—
October	79	—
November	56	—
December	30	—

It is not considered that any of the traps yet invented are likely to bring either *G. morsitans* or *G. swynnertoni* at all near to extermination—or to affect *G. brevipalpis* at all. A number of traps invented are useful against *G. pallidipes* and *G. palpalis*, but for these species also complete extermination, if such is needed, as in most cases it is, is unlikely to be brought about by trapping alone. Hand-catching off screens, which is much more effective, failed in more than a year to exterminate *G. swynnertoni* in Block 5A, but hand-catching has brought *G. palpalis* practically to extermination in the "blocks" on the tributaries of the Kuja—traps having been less fully effective. Scent extracts from animal glands may make all the difference, but despite large quantities collected lately by Blunt and Gabbutt, it has continued impossible up to the time of writing to test them properly owing to shortage of staff.

The fact that traps will catch well when first set out and will then, con-

tinuously, catch less well, even in the absence of bleaching, has been noted repeatedly both by ourselves and by C. W. Chorley in Uganda. The general results on Maboko Island (pp. 440–443 below) seem to fit in with this phenomenon and it has seemed even possible that in such a case as the latter we are exercising a selective influence, *i.e.* a strain of fly that readily goes into the traps is being rapidly eliminated in favour of a strain that does not.

B.—INDIRECT ATTACK ON THE TSETSES BY MODIFICATION OF THE COVER.

1.—THE ELIMINATION OF TSETSES BY THE DESTRUCTION OF ALL BUSH.

Concentrated native settlement, resulting in the felling of all trees indiscriminately, as it at present does, in the destruction of the grass, and the production of the vast over-grazed and eroding spaces to be seen to-day in Mwanza, Shinyanga, Singida, and other cultivation steppes (pl. 18, fig. 2; pl. 19; and pl. 20, fig. 1), may conduce to ease of administration but is a lamentable event. Wholesale clearing of country for the expulsion of fly is equally reprehensible where it is not vital for sleeping sickness purposes or does not merely form part of a tsetse barrier scheme; it is also extremely expensive.

Progressive eating into the margin of a fly belt by a great native settlement alongside is again wrong, where anything better can be done. It is simply, as stated already, the growth of a cancer. If the bush were allowed to regenerate behind as the population advanced that might be comparable with a ringworm, but it would at least be less ruinous to the country-side than the other. In view of the fact that the Tsetse Research Department has been accused in the past of carrying out such clearings, though actually it roundly condemns them, attention is drawn to maps 2 and 3 and to the fact that the clearings that are the work of the Department are in nearly all cases not wholesale clearings of large patches of country but barrier-clearings cutting off country which is then attacked otherwise, without wholesale clearing of the bush. Here and in the Lake Province generally they form part of a definite plan.

Our own chief delinquency was the clearing of "Kizumbi Bay" in 1924, but it was done with a propagandist object, as a grand start-off to the first tsetse campaign, to stay a retreat, to show the tribe what with an effort it could do, and to ascertain by experiment whether it would do it; and it was used as a radiating-point for the barrier clearings which even then were our prime object.

We have already learned, as stated many times above, that each tsetse is usually dependent not on one bush type only but on obtaining access, as it requires it, to each of two or three types. It would seem likely, therefore, that wholesale clearing would be wholesale waste of time, when we may be able to get rid of the fly as effectively by merely destroying or modifying one of the bush types that it needs. How this perhaps may be done is described below under sub-section 3 "discriminative clearing" and sub-section 5 "not burning the grass."

2.—ATTACK BY MERE ISOLATION OF SPECIAL VEGETATIONAL AREAS.

(a) Unsuitable types of wooding.

The types of wooding that are unsuited to the various flies have been listed already under each species. To recapitulate briefly, it is believed that

the following types can only be infested, seasonally or by infiltration, when they are in contact with more suitable wooding.

In relation to all tsetses: (i) Gall-Acacia (" Ilula "), consisting of any of the following species—*Acacia drepanolobium*, *A. formicarum*, *A. seyal*, *A. malacocephala*, *A. Burtti*, *A. zanzibarica*—often with a small admixture of other trees such as *Albizzia hypoleuca*; where the other trees begin to predominate the rule no longer applies; and (ii) almost certainly, the more open *Terminalia torulosa-Protea* types such as occur at Babati.

In relation to *G. morsitans*, additionally:—(iii) The drier types of thorn-bush or nyika; (iv) continuous closed forest and thicket, whether evergreen or deciduous; (v) particular areas of the miombo itself; and (vi) areas of pure tree-Combretum.

In relation to *G. swynnertoni*:—(vii) The open type of *Commiphora Schimperi–Combretum Zeyheri–Acacia stenocarpa* wooding occurring at and over 6,000 feet, referred to on p. 384 below; and (viii) thorn-bush generally that is completely devoid of thicket, if game be not abundant; (ix) all extensive miombo in addition to the above; and (x) continuous dense thicket areas.

In relation to *G. pallidipes*:—(xi) Country devoid of good thicket and especially riverine thicket.

In relation to *G. austeni*, *G. palpalis*, and *G. brevipalpis*:—(xii) Country, or, for *G. palpalis*, lake or river banks, devoid of a heavy thicket element.

It is probable that the making of an effectively wide barrier-clearing between any large areas of one of these types and the main fly bush will free the former permanently of the tsetse fly indicated.

(b) The Huruhuru experiment.

Our first large experiment in the clearing of an area of fly by isolating it was concerned with the great Huruhuru mbuga system. Much of this is open but much more carries wooding of well-developed gall-acacia (young gall-acacias are seen in fig. 32). This in the past had been infested, as we knew from observations of isolated areas, solely through its attachment on various sections of its periphery with the typical strongly-infested *swynnertoni* thorn-bush of Shinyanga on the south, and on the north, in Buhungukira, with wooding of *Ostryoderris* and other genera infested in part with *G. morsitans*, in part with *G. swynnertoni*.

As is stated more fully under Part 6 (pp. 385–394 below) the connections with the fly bush proper have now been cut along a considerable proportion of the periphery. The flies in the gall-acacia wooding have already come down in consequence to a mere odd occurrence, and 25,000 head of native cattle have been utilising the wooding successfully. It is hoped, with the completion of the work, to bring about elimination of the tsetse throughout this mbuga system except in certain " islands " of typical fly bush on which future attack is planned and which in the meantime will have to be avoided by cattle (see map 3).

(c) Block 7A in Shinyanga.

The flies (*G. swynnertoni*) have become very scarce in this block since we separated it by a clearing from Block 7C. The latter differs from the former mainly in the possession of much *Acacia mellifera*.

(d) Possible further measures on the same lines.

Captain Findlay is at present due to carry out a survey of a great shelf of type (vii) above, overhanging the east side of the Yaida depression, with a

view to deciding whether its detachment is worth while and is within the man-power of the Wambulu.

Jackson's extensive survey in the Tabora area has been carried out partly with the object of finding a large piece of type (v), the isolation of which would be experimentally feasible and practically useful.

An area of type (viii) exists ahead of the *swynnertoni* fly advance near Lake Basotu with so little thicket that the clearing of what there is will not be a great task. It is partly cut off already by Gordon-Russell's clearings. Additions to those clearings may make the undertaking feasible and at the same time stop the fly advance, though an alternative measure is also envisaged.

The making of the barrier clearing effective is of course, in each case, the main difficulty. Where this can be done the measure should be valuable, reclaiming, as it will, a great area of ground with relatively little clearing, especially if natural barriers can be found and worked into the barrier.

3.—ATTACK BY DISCRIMINATIVE CLEARING, WITH BURNING OF THE GRASS UNCONTROLLED.

(a) The history of the measure.

The view that clearing the essential dry-season concentration sites of *G. morsitans* might alone destroy that species occurred to the first discoverers of the fact that that fly did so concentrate, namely, Jack and Shircore, and was suggested in some detail by the latter (1914). It was subsequently discussed by myself (Swynnerton, 1921) and more recently it has been the subject of promising or successful experiment by ourselves in Tanganyika and by workers in Nigeria. The narrow long-shore clearings made by Fiske and Carpenter against *G. palpalis* rather come into this category.

That even less than this might achieve the effect desired was present in the view of the early workers on *G. palpalis* on Lake Victoria that clearing of the undergrowth only might suffice to remove that fly—a conclusion that was strongly borne out by what happened when, left to themselves, the situtunga antelopes cleared the undergrowth (fig. 17). The same conclusion struck me also on finding that *G. brevipalpis* and *G. pallidipes* were dependent on the thickets occurring, both scattered and in stream-fringing forest, in the matrix of miombo savanna which formed their general habitat in the area, which I investigated in Mozambique. This led to what was probably the first experiment anywhere carried out in the clearing of a single element in one only of the vegetational communities that were essential to a fly (Swynnerton, 1921). Only the undergrowth "furniture" (fig. 13) was removed, leaving all trees, large and small, standing, and *G. brevipalpis* at once disappeared. From the lighter scattered thickets outside *G. pallidipes* entered, but the proportion of females taken by means of bait-cattle suggested that it was using this partly cleared ground as a feeding-ground only, and that the clearing of its own lighter thickets would have also resulted in its disappearance.

Discriminative clearing was, therefore, from the first, given a place of importance in our programme of observation and experiment. Our organised fires were regarded as a mode of discriminative clearing, attacking as they do in some types of country the thickets. Block 1 in Shinyanga was cleaned of flies in 1924 through clearing the scattered thickets only, followed by fire, and Blocks 2 and 6 in 1924–26 through attack on the small, scattered thickets

by organised burning only, the general wooding not being touched, though some of the acacias died. In the case of each species of fly, observations are being made to ascertain whether and where it concentrates for any part of the year, and what seem to be the most cheaply removable constituents there of its habitat, the destruction of which would be likely to disturb it adequately.

FIG. 16.—The furniture of a rest-haunt and breeding-place of *G. brevipalpis*. On the furniture only being cleared, the flies deserted that portion of this gallery forest.

Further experimental clearings are being carried out on *G. swynnertoni* and *G. pallidipes* in Shinyanga, both with grass fires and without them. That much more has not been done on this last species, and on *G. brevipalpis*, *G. austeni*, and *G. morsitans*, has been due to shortage of funds.

(b) The different types of discriminative clearing.

The object in all our discriminative clearing, it may be repeated, is to clear as little as is necessary of one vegetation type only in those spots only which are essential to the fly at one season only of the year. To this our investigation is directed. Discriminative clearing may be of two chief kinds, (i) for use with organised grass-burning (pl. 14, fig. 1), (ii) for use with uncontrolled native burning or (for some species of fly) without burning. The first is dealt with elsewhere (p. 296 below). We know already that the clearing of thickets and of hard-pan wide enough to harbour flies fleeing before an organised fire is effective in well-grassed savanna.

As regards (ii), viz. discriminative clearing used by itself with mere uncontrolled native burning of the grass, this might take one of four forms :—

(i) the feeding-grounds may be cleared;

(ii) the rest-haunt and breeding-ground may be thinned to the point of giving inadequate protection to the fly from desiccation, etc., by (for example) the destruction of the most cheaply-cleared elements;

(iii) the "furniture" of the breeding-grounds (fig. 16) may be destroyed;

(iv) the feeding-grounds, rest-haunts, breeding-grounds, or furniture, at the dry-season concentration sites only, where such occur, may be cleared or be so modified by partial clearing that the flies will not find them adequate in all essential respects.

Where it is a case of clearing elsewhere than in a focus that is naturally isolated for part of the year it will be necessary to place an effective barrier between the areas discriminately cleared and the general fly bush; otherwise the flies will pass into and take up their quarters in the country that is untreated and will still come out of the latter and infest the areas treated, just as to-day they use the woodland communities that by themselves do not suit them until we place a cleared barrier between. An exception is the dry-season concentration that is separated from the next one by a considerable expanse of bush that in the dry season forms a barrier and is suited to alternative (iv).

(c) The applicability of each of the varieties of discriminative clearing suggested above.

The applicability of each variety of discriminative clearing in relation to each important fly appears to be roughly as follows :—

(i) *G. morsitans.*

The clearing of the mere feeding-grounds, at any rate without settlement following, may merely put back their margins.

The breeding-grounds, except those that are included in the dry-season primary foci, are commonly coterminous with the general wooding for some distance back from all feeding-grounds. The effect of thinning this wooding in country of the type of Sambala (see p. 77) would be to spend a large sum of money and furnish the flies with a considerable extra supply of breeding logs. Where limited and widely separated dry-season foci are the rule the measure should be much more feasible.

The clearing of furniture from a *G. brevipalpis* rest-haunt and breeding-ground was effective, as described above (fig. 16). The clearing of the logs from a *morsitans* "home" at a concentration site has not been tried. Rot-holes and interstices between root-bases would have to be dealt with also, and the presence of large rock outcrops might nullify the effect of such a measure. It has been suggested that these might be blocked. It was suggested many years ago that a cheap chemical might be mixed with the soil of the breeding-sites that would destroy the pupae. While either of these things would be possible on a small scale there are very few places in which sufficiently few breeding-sites serve enough country to make their treatment inexpensive.

The clearing, even the partial clearing, of an essential element in the primary dry-season concentrations, in country the rest of which is evacuated at that time of year, should be highly effective, and Jackson has been engaged on a study of the Tabora fly belt with a view to the choice of a site for a thorough-going experiment of this kind. An experiment in the complete clearing of dry-season haunts has been carried out in Nigeria with success under conditions

of greater desiccation and dry-season vegetational contrast than obtain in Tanganyika; and Jackson finds that an interzone of a distinctive (and readily cleared) vegetational type characterises all true concentration sites in South Tabora.

This, if more widely confirmed, may be a very important observation. Jackson has found, very generally, the following contrast in situations in South-east Tabora:

(α) *Areas unsuited for concentration of* G. morsitans.

A piece of country, approximately 50 miles across, was examined at different times in the dry season, and also after the break of the rains, in 1934. It was re-visited in May 1935. The southern part of the area was composed of a plain, on which stands of *Isoberlinia globiflora*, or alternatively *Brachystegia Boehmii*, up to half-a-mile across, interspersed with clay-soil "mbugas" with more or less sandy wash. The mbugas supported *Acacia formicarum* (a gall-acacia), *Combretum ternifolium*, *Crossopteryx febrifuga* and other small trees. Thickets were few and small, except on a stream traversing a portion of the area, on which *Diospyros*, *Mimusops* and other large trees overtopped massive thickets of *Canthium*. The interzone element to be mentioned below was absent.

Sable and roan antelope, Lichtenstein's hartebeest, southern reedbuck and oribi abounded, while common duiker, steinbuck and topi were not rare. *G. morsitans* was almost entirely absent both from the mbuga and the wooding; certainly not a dozen being taken on twice that number of visits, whether on foot or by lorry. Empty pupa cases (30 including a dead pupa), were, however, taken along a mile length of the stream, indicating seasonal spread down it from the more favourable area to be mentioned, probably about July.

Other country, of similar type, occurring freely elsewhere through South Tabora, is equally devoid of any concentration of *G. morsitans*, though game is usually numerous.

(β) *Areas suited to concentration of* G. morsitans.

In the country to the north, where the miombo was separated by inter-zones of acacia and other types, with thickets, from the drainage valley-bottoms, concentrations of *G. morsitans* were found. In no instance was game nearly so often seen as in the country just described. Thus sable antelope, hartebeest, steinbuck and topi were never seen near the concentrations, and oribi was rather rare. Greater kudu was, however, seen once, and roan antelope and reedbuck were fairly frequent. To one of these concentrations many visits were made, and fly rounds and reconnaissances were carried out in it from August to November and in May. The apparent density of mature male *G. morsitans* in this concentration reached about five per minute of collecting, the density depending on season. Both live pupae and empty cases were taken in fair numbers in August and in October. There was much thicket on a stream.

The presence or absence of the inter-zonal strip combined with a difference in the amount of thicket has constituted the main distinction between the country used and the country not used by the flies. This suggests that the destruction or modification of these elements, where they occur, might suffice to get rid of *G. morsitans* in the conditions obtaining in South Tabora.

Nash (1935), following his experiments (p. 188 above) on the effect of high shade temperatures on *G. submorsitans* and *G. tachinoides* in northern Nigeria, where these flies live close up to their thermal death point, makes the highly

interesting suggestion that the removal of the marginal thickets that exclude the dry wind from the dense forest patches that they take refuge in, may so desiccate the latter as to exterminate the flies.

(ii) *G. swynnertoni.*

The feeding-grounds of *G. swynnertoni* are open mbugas, and, as in the case of *G. morsitans*, their clearing and that of their margins might often merely put the latter back without affecting the survival of the flies.

On the other hand, the hard-pan strips are in use as concentration grounds all the time, and the complete clearing of these, with their thickets, has been attempted already with results that are very striking. Mere thinning of these strips is (*a*) hardly worth while, for the wooding that stands on them is already extremely sparse and easily cleared, being mainly soft-wooded *Commiphora Schimperi* and *Lannea humilis*; and (*b*) the mere thinning of the thickets, which afford the main clearing problem here, and even their practical removal, has proved not to be sufficient in practice, and regeneration is in any case immediate. There is just an indication that clearing of the trees and not of the thickets might be effective, and this is being put to the test.

The flies, where in great density, breed in the thickets on eluvial soil and those on or beside hard-pan and mbuga indiscriminately. When in less density they tend to concentrate on the thickets of the last two, and it is probable, therefore, that if a start were made under conditions of high density, the clearing of these alone would sooner or later—in a season unfavourable to the fly—prove effective. One cannot, however, clear long beforehand against such an event without being prepared to re-clear the regeneration each year till the unfavourable season arrives.

Thinning of the general bush could be attempted by the clearing of the soft-wooded *Commiphora Fischeri* and one or two other species, but it is certain that with uncleared hard-pan present as a refuge it could not succeed; and the clearing of the hard-pan, which in most places is far less extensive, promises at present to suffice.

The destruction of the "furniture" only, in the case of *G. swynnertoni*, amounts once again to the thickets. Most pupae are found under logs and lianas in the thickets, but the bases of the many-stemmed *Grewia* and *Abrus*, forming the thicket, are able to suffice in themselves, so that the removal of the thicket seems necessary. Vicars-Harris, however, in the course of his fly rounds in Shinyanga, believes he has found indications that this "sufficiency" may not be complete in all months of the year, and has suggested blocking of the types of breeding-site which then temporarily become of importance.

We have found no such marked seasonal concentration grounds for this species as in the case of *G. morsitans*. It seems, therefore, that it will be necessary to clear all thickets or to clear all hard-pan areas. Nothing so economical seems practicable as the suggested procedure against *G. morsitans*, unless in conjunction with not burning the grass, a possibility which is discussed on pp. 272–275 below.

(iii) *G. pallidipes.*

This fly inhabits a greater variety of country than either of the two flies just dealt with, and each situation will have to be diagnosed individually. In most country the clearing of riverine thicket (though by no means necessarily all of it) would seem to be the greatest blow that could be dealt to this fly in the matter of discriminative clearing. Curson's description (1924 : 449) of

the observed attacks of this fly on bait-animals is probably indicative of the usual position in dry country. "The further . . . from the river, the fewer the flies that attack, until eventually, when the outskirts of the bush-veld are reached only an occasional fly is seen. . . ." Dozens of trips with oxen at all hours and at various times of the year from the river to the edge of the wooding and in the opposite direction fully confirmed the above.

It is further possible that clearing, within the riverine limits, will sometimes have to be wholesale, for I have found *G. pallidipes* sheltering and breeding in very small thickets indeed, but there are indications that different thicket types are used, under some conditions, at different times of the year, and the probability is, therefore, that less than complete clearing in the denser of these will suffice provided that we can keep down the regrowth till the fly has been exterminated. That this will prove the great difficulty in all fine discriminative clearing is indicated from our experience in Shinyanga, from the position in the Muheza (Tanga-Nyusi) area described on p. 176 above, and by the further fact that, when visiting the Lambwe Valley in Kavirondo, I noted that the clearing being made there through thicket with all the labour that was available was already at one end up-grown and reinfested by *G. pallidipes* before it was completed at the other.

Burtt, when investigating the serious threat by *G. pallidipes* to the Mpapwa Veterinary Station, concluded that the wooding of the Matamondo stream was the trouble and that seasonal spread of the flies took place along it. The effect has therefore been tried, in the first place, by the Veterinary Department on Burtt's advice of putting mere barrier clearings across it, to check the free ranging of the flies. Being close to the Veterinary headquarters, the situation is capable of being watched, and, with further steps which may progressively be taken, will provide a useful experiment. It is a form of discriminative clearing and the initial results, from very small clearings, seem most promising (*cf.* Veterinary Department's annual report for 1933 : 19–20 and pp. 340–345 and p. 379 and p. 380 of the present paper and fig. 23).

(iv) *G. palpalis.*

The long-shore clearing already used in Uganda and elsewhere is itself discriminative clearing on very broad lines, and is effective. Where there are connections between the shore and the wooding stretching back over the land, *G. palpalis* sometimes uses the latter to very great depths, if suitable food is present. Here clearing, if relied on alone, could hardly be less than wholesale within the usual, narrow, long-shore limits without perpetuating the stretches or bridges of open bush facilitating contact of the flies with the water—their best chance of indefinite survival. As regards flies that are purely "long-shore," the thinning of the more massive wooding, where this is so confined to the shore or so patchy as on Maboko Island, might suffice. Its mere isolation from the feeding- and breeding-grounds under the common Uganda conditions would be useful, if one could be sure that the isolation would be effective, namely, that the flies would not still be able to utilise both needed types by crossing the clearing by following along the shore line, a thing that, when hungry, they would do.

In the above we have again the problem of maintaining expensively a partial clearing until all the flies are finished.

(v) *G. brevipalpis* and *G. austeni.*

Both these species (as well as the others) need further study in this connection. In the "man-made fly belts" described in Part 2, Section N (p. 176

above), the destruction of the rubber and other tree plantations would probably be needed to get rid of these flies; and they would still survive at the contacts with rain forest on the slopes of the hills. Destruction of the undergrowth in the plantations would be an immense task and would hardly be effective, for the regeneration of the rubber is too prompt and quick-growing. The Lambwe Valley incident, referred to above, would be repeated, unless settlement were introduced or sisal (shall we say) planted over the acres cleared.

At the rain-forest contacts we could not thin into the forest without making it more suited to the flies. Where, however, these species occur in smaller and more broken coverts in savanna and in riverine forest or thicket the prospect of exterminating them by discriminative clearing would seem good. The successful experiment in expelling *G. brevipalpis* from gallery forest by merely removing the "furniture" has been referred to more than once, as has fig. 13, which shows the site.

(d) Further actual experiments.

(map 2.)

The sites of our experiments in Shinyanga against *G. swynnertoni* by means of discriminative clearing have been :—

(i) *Block* 5A (pl. 13, fig. 1).

A remnant of the flies continued after organised grass burning and screen catching and a large re-incursion also took place. The measure that finally succeeded was complete clearing of the hard-pan strips.

(ii) *The outer circle.*

Here fire was used as well, seeing that the country was needed urgently for settlement, but it has been possible to distinguish the effect of burning from that of discriminative clearing.

(iii) *Block* 5B (pl. 14, fig. 1).

Nearly all thickets and some of the trees of the hard-pan were cleared in 1932–33. Despite the attachment of 5B to the untreated and well-infested Block 11 on a long front, the fly numbers fell very greatly and have remained low ever since. Now that Block 11 is being attacked by not burning the grass, it is hoped that it will not be necessary to clear Block 5B, and a further instalment of discriminative clearing of the concentration sites has been proceeded with in that block.

(iv) *Block* 7C.

This block has been the site of a detailed botanical and entomological study, in order to ascertain whether there is a possibility that even less clearing than is entailed in the experiments already in hand may not serve. Further experiments will be inaugurated.

(e) Limitations deduced from the work on *G. swynnertoni.*

This form of attack on *G. swynnertoni* seems likely to be feasible (i) where the amount of clearing entailed is not too great (in Block 9 at Shinyanga the hard-pan and its thickets are so generally distributed that the clearing of nearly the whole block would be necessary); and (ii) where the blood supply is not so ubiquitous and abundant and permanently present as to enable the

flies to dispense with the concentration grounds. It will be recalled (p. 99 above) that during a brief inspection of the position at Banagi, on the edge of the Serengeti plains in December 1933, I found the flies living and breeding not

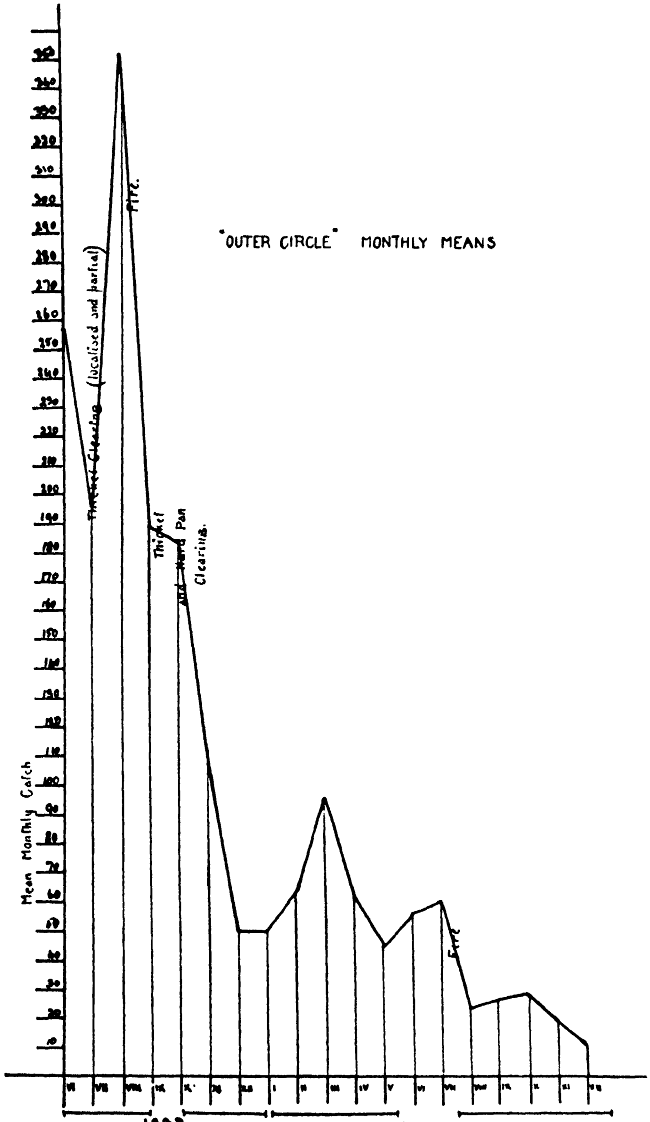


FIG. 17.—The freeing from tsetse, *G. swynnertoni*, of the "Outer Circle," Shinyanga (see map 2). A very limited discriminative clearing was followed by a fall from which recovery took place. An organised grass fire which brought the number down was reinforced by further clearing of the hard-pans with their scattered thickets and trees, and the fall continued. Further slight rises were shown, by picketing the paths, due to reinforcement from outside, the control of which completed our measure.

in thickets only, but in very open wooding at the foot of *Acacia* and *Balanites* trees, a position which will probably not often confront us. This form of attack will only be feasible for *G. swynnertoni* where we are attacking a whole fly area

at once or are prepared to place an impassable barrier between the block that we are attacking and the rest. This species goes out freely in numbers into the smallest cover, even into the mere light litter of felled gall-acacia lying far out in an mbuga, and it will use as a stepping-stone all partly-cleared bush from which it is not adequately barred.

Our experiments in Shinyanga show already that, working on anything larger than an experimental scale, the amount of clearing will have to err on the large side and be sufficient everywhere to exterminate the flies in one season, for, as indicated several times already, without organised grass fires regeneration of thicket will take place and the flies will soon find conditions to suit them.

The combination of details that will have made a site suitable for the flies' habitation will vary from place to place. There may also be conditions (such as abnormal abundance of food) that, as at Banagi, and as in Burtt's observation on *G. austeni* near Morogoro (p. 120 above), will render one type sufficient. Exactly what and how much will have to be cleared to make a site unsuited to the flies with a minimum of expenditure, and also without making it suitable for other species of tsetse that may be near, will therefore be a matter of long observation and practice. As regards fine discriminative clearing one cannot put a battery of meteorological instruments into each thicket of differing type in a locality and say, here clearing of half the stems, and here of a quarter, will result in too high a temperature or low a humidity and the flies will die out. Questions of amount, extent, mechanical practicability, regeneration, and expense, require to be considered, as do the selective reactions to the measures of the flies and the reactions on the part of the plant elements that are left; for the latter may with their branches at once occupy the spaces left vacant and perpetuate the former conditions. Very fine discriminative clearing may be useful when the flies are living under conditions that are very nearly lethal. Otherwise it is a rather complicated measure, and only broad discriminative clearing is likely therefore to be usefully effected by the type of labour commonly available with the supervision that can be given on the scale that the operations will demand.

Discriminative clearing, not too fine, has produced wonderful results against *G. swynnertoni* and seems a most promising measure against *G. morsitans* for very great areas of country.

4.—ATTACK BY DISCRIMINATIVE SETTLEMENT.

In a memorandum which I wrote a few years ago, I urged the usefulness of placing concentrated settlements at the fly's concentration sites. The settlement of all such sites throughout a piece of country would quite likely have the effect of eliminating the tsetse and, in the meantime, of reducing the infestation in and around the settlement. Settlements situated, as many are at present, in the general wooding are subject to infestation by the flies that are based on the feeding-grounds, or in the dry season on their "foci," a little way off. The greater such a settlement, the greater the opportunity lost for freeing a piece of country of fly. Concentration of population is likely to take place in the *morsitans*-infested *Brachystegia* wooding of Handeni; I am recommending (*see* p. 351 below) that it shall take the form of a network following the valleys only and be nowhere so broad as to be wasteful.

We were able to carry out one experiment, in this case only on a feeding-ground. This was at Selya in Kondoa–Irangi. Selya is a lake and swamp, the latter inhabited by a herd of buffalo and its edge formerly a strongly-marked

feeding-ground. The latter was cleared and settled and the feeding-ground, as such, disappeared, though the buffalo remained in the swamp. Funds for clearing were insufficient to enable us to attack the other important feeding-grounds of the neighbourhood, so the general infestation continued, but the settlement that eventuated at Selya had produced a hopeful result.

Most of the sleeping sickness settlements that have been created in the various Territories appear, from the point of view of tsetse control, for which they might have been useful, to have been very largely wasted.

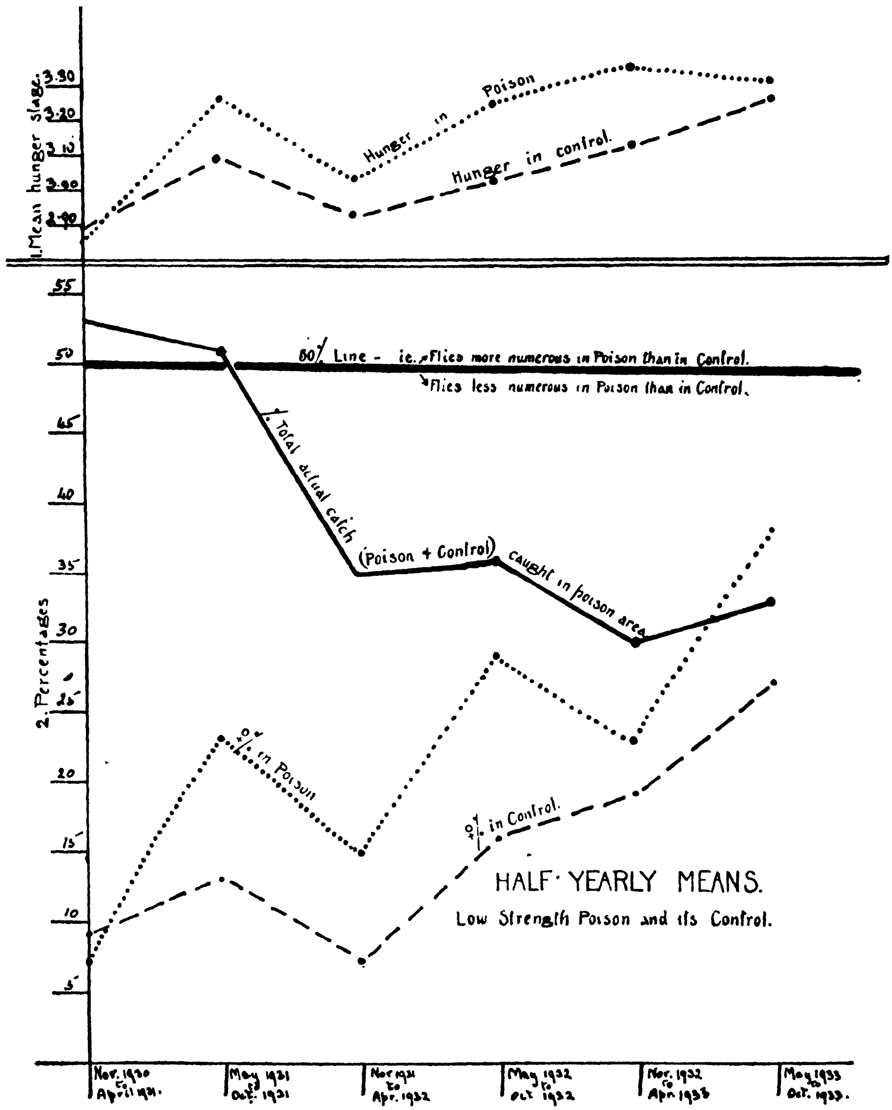


FIG. 18.—The effect on *G. swynnertoni* of defoliating the trees and clearing the thickets in half of a selected portion of Block 11 in Shinyanga. The flies taken in the poisoned area were hungrier than before and than in the control, the percentage of the total catch taken in the poisoned area fell considerably, and the female percentage rose. More and more it took on the character of a feeding-ground.

5.—ATTACK BY LONG-LASTING DEFOLIATION.

Fig. 18 illustrates an experiment by Napier-Bax in Shinyanga on the effect of defoliating the wooding over a square mile of woodland by means of a low-strength poison (arsenic pentoxide—*see also* p. 412 and fig. 29). It proved a cheap method of partial clearing: many trees were killed and the rest, defoliated and killed above the cut, were slow in regenerating.

Briefly, the effect on the flies was as follows:—As soon as the leaves dried and began to fall, the numbers of flies coming to man in the poison plot rose compared with those in the control plot, which was contiguous with it; hunger rose also. Later, hunger rose further in the poison plot, while numbers began to fall. The ultimate position was a partial evacuation of the poison plot in favour of the control, with high hunger in the former, until the rains. In the rainy season, when to the eye the difference was *greatest*, there was *least* difference between the tsetse of the two plots.

The extension of the measure to further country adjacent had a very marked effect, and there can be no doubt that with the measure applied on a larger scale the whole area would become free of tsetse without extermination of the bush. It might also be used for discriminative clearing without felling and at much less than the expense for full-strength poisoning.

6.—ATTACK ON *G. SWYNNERTONI* BY NOT BURNING THE GRASS FOR SOME YEARS.

(pl. 12, figs. 1 and 2.)

(a) The experiments.

Fires have been excluded (i) from Block 4A in Shinyanga, a block of country of four square miles, infested by *G. swynnertoni* and a few *G. pallidipes*, for four years in succession; (ii) from Block 10A, of two square miles, infested by the same flies, for three years; (iii) from two "barrier" strips following roads that previously were highly infested by the same flies—for four and five years respectively (*see also* pp. 316 and 324 below); (iv) from Block 11, of nearly 70 square miles, during 1934–35; (v) from an area of 150 square miles in the Maswa district, also during 1934.

In the control block in Shinyanga, Block 4B, of only 1¾ square miles, the grass has been burned in the ordinary native fashion annually during the period. The same applies to Block 9, of 55 square miles, which is being used as a temporary control.

(b) The effects in the first year.

On the vegetation. At the end of December in the first year of non-burning—*i.e.* from four to six months from the first omission and from sixteen to eighteen from the last fire—woody regrowth, previously kept down by the fires, has already in each case made good headway as against that of the burned control; but the main difference is that the green grass nearly everywhere is growing up through a mulch, thick or thin, mostly the former, but sometimes destroyed by termites, of the previous year's dry grass. This keeps the soil surface damp between showers, the more so doubtless since run-off is checked. The miserably grassed hard-pan patches remain exactly as before and with no old grass visible, but each is hemmed in by the grass-mat conditions of the rest of the country. In the controls this is absent and, instead, much bare ground is present between the tufts of the grass.

On the game. As yet no effect has taken place. Block 11 to-day contains

numbers of game of the same species as formerly and, with green grass everywhere abundant, they have not even collected on the fire-breaks.

On the fly. In every experiment the fly density has failed to make its usual end-of-year rise in the unburned ground generally, miles wide though this may be. In Block 11 it had in December 1934 collected in great numbers on the burned median fire-break. When this same block was unburned for one year only in 1930 the flies failed to accomplish the rise in density that characterises the short rains and short dry season, but rose normally on the advent of the following long dry season.

(c) The effects after a period of from three to four years.

On the vegetation. In the four earlier experimental blocks and strips, but not in the controls, extensive thicket, much of it already quite high, is growing up everywhere in the grass of the savanna as a result of the exclusion of the fires, except where a ferruginous underground crust keeps spaces open between thickets. Thus the previous marked difference, both spatial and seasonal, between the respective densities of the different vegetational communities is disappearing. Herbaceous climbers (Convolvulaceae) are matting the thickets and all the adjacent grass. Much grass-country remains, and in this the grey grass-mulch is still a strong feature, but it is perhaps less generally dense than in the first year—for in places it has rather choked down fresh grass-growth and is itself diminished in consequence; but elsewhere, and especially in long-grassed mbugas, formerly seasonal feeding-grounds, it remains much as before. The grass-country referred to is broken into patches, mostly small, by the ever-growing network of thicket. The centres of the old hard-pan concentration grounds remain as before, but longer and denser grasses appear to be invading them very slowly from the edges, and thicket of *Ormocarpum* and *Dichrostachys* is encroaching on them.

On the game. In each of the long-unburned blocks game in the aggregate is about as plentiful as it was from the first. It is apparently changing specifically, a recent survey by Commander Blunt having shown that impala are much more abundant now in the burned control (Block 4B), greater kudu and giraffe in the unburned Block 4A. In Block 10A (unburned) wild ungulates during the year 1934 have been 194·5 per 10,000 yards of transect. In Block 9 (burned as a control), 63·2 per 10,000 yards.

On the fly. The highly satisfactory position in the two barrier strips is described on p. 316 below. In Block 4A the general tsetse density, as indicated by the regular fly round, decreased in three years by about five-sixths. A small rise in the dry season of 1934, bringing up the figure for that year, may have been due to the extreme drought in that season combined with the tendency of the flies to enter thicket under those conditions—entering here from Block 4B.

TABLE 49.

The effect on a population of *G. swynnertoni* of excluding grass fires.

Flies per 10,000 yards per round.

	1929–30.	1930–31.	1931–32.	1932–33.	1933–34.
Block 4A	69·0	61·5	17·5	11·9	13·2
Block 4B (control)	28·5	29·8	56·6	85·6	115·0
Ratio 4A : 4B (very roughly)	2·5 : 1	2 : 1	1 : 3	1 : 7	1 : 9

"The populations of 4A and 4B were estimated in June 1934 by the Survey Entomologist's Recovery Ratio method. That of 4B (1¾ square miles) was found to be about 9,000 flies [*G. swynnertoni*] and of 4A (4 square miles) about 1,000" (Potts, annual report, 1934).

Actually this gives a ratio between the treated block (4 square miles) and the control (1¾ square miles) of 250 : 5,143 per square mile or approximately 1 : 20. This represents less than half the difference obtained from the fly rounds of that month (and of 1933–34), but this round undoubtedly passes much too close to Block 4B, and a new round that is now being started is expected to give the true picture, as well as, by comparison, reinforcement of the strong evidence already available as to the likelihood that a large proportion of the present flies of 4A are immigrants from Block 4B.

The above refers to the whole population of the block. The number of the flies in the hard-pan in Block 4A, considered alone, has recently been shown to be down by one-third only. This reduced population, representing the "economic density" of the block (*cf.* Elton, 1933), appears to have become moderately stationary.

(d) Discussion of possible reasons for the more general effect on the fly.

Factors that may contribute to the destruction of a population are (*a*) lethal and (*b*) deprivative.

In this instance there is no evidence that lethal factors have been operative. None of our observations suggests that birds or insects predatory on tsetse, or any fungus, have been at work. There is definite evidence that starvation, due to poor visibility or reduced activity, is not the cause—for the flies taken in Blocks 10A and 4A are always normal as to nourishment, and the captures show the type of female percentage that is always associated with the presence of food.

Of the deprivative factors—Leopold's "welfare" factors (1933)—humidity such as might deprive the fly of its ability to breed is, just possibly, present; the general stimulus, of whatever it consists exactly (*vide* Swynnerton, 1934 : 420 and 427), which, at the moment when the fly population has reached its lowest ebb each year, comes with the early rains and sends it soaring sensationally upward, is obviously lacking; and some wet-season immobilisation of the tsetse may be present through the surviving grass and tree savanna being cut up into little patches by a network of thicket.

The effect, as just indicated, is manifested graphically mainly in the failure of the density curve to soar on the advent of the early rains and in the short dry seasons. Having failed to rise at this time, it continues low or falls further during the later rains, rising somewhat in the long dry season. It is interesting therefore to note that the contrasts, as evinced by apparent fly density, between burned country and unburned are especially strong in the short wet season.

On the unburned ground the water-content of the soil is increased in the early rains, dampness is retained between showers, the temperature is lowered, evaporation is reduced, and light intensity in the grass becomes less (Scott, 1934). Perhaps a pall of somewhat greater humidity tends to hang over the ground and after the first year is assisted to do so by the interference with the free movement of the air that is exercised by the network of thicket. Things apparently small may affect the breeding of animals, and laboratory work (Buxton in Nigeria, Potts in Tanganyika) already suggests that dryness is a stimulus to the breeding of *G. morsitans* and *G. swynnertoni*.

Of the reactions of the flies to the deprivative factors concerned, it might be suggested that these last, causing some sort of discomfort, might have caused the flies to emigrate into Block 4B, the only semi-accessible alternative. Actually marking experiments have shown that passage still takes place. But Potts has pointed out that "if the flies had been leaving Block 4A and had thus been responsible for the rise in the numbers in Block 4B, one would expect that rise to have slackened now that the decrease in Block 4A has ceased. Such has not been the case." On the other hand, if the effect is on the breeding, distress among adult flies in Block 4A would not be detected, and the result might have come about by sheer lack of replacement independently of any emigration. If the persistence of a small fly population in Block 4A were due even now solely to reinforcement from Block 4B, this would be compatible with the fact that such rise as takes place is solely in the dry season when the leaf is off the thicket and when only (as Burtt showed) the fly tends to traverse it.

It is suggested by the general results so far on the tsetse, and by the present appearance of the country in the four older experiments, that with the extension of the advance of the vegetational succession towards its natural climax on the obstinate hard-pan also the present fly population will dwindle further and disappear if the areas are fully isolated; the growing homogeneity in the density of the whole vegetation will reach a point at which it is unlikely to satisfy the daily and seasonal needs of an insect which for food, breeding, and regulation of moisture and temperature, has a separate and vital use for each of the three densities and eco-climates furnished by thicket, savanna wooding and nearly open hard-pan and vlei, and which concentrates at their contacts.

The work still being done in the laboratory (pp. 177–195 above) and the study of eco-climates in the field (p. 43 above) will doubtless supply the explanation for the reduction of the tsetse outside the hard-pan.

(e) Limitations of the measure.

The hard-pan, as in all our attacks on this fly, remains the difficulty. It will doubtless be encroached on slowly by successional invasion of the classical type from outside—by grass-built humus increasing and supporting ever better grass, and then shrubs, but the process will be slow. We must hasten it if we are to shorten and cheapen the process of holding up the grass fires. The following measures are possible :—(i) the hard-pan areas may be cleared of their scattered trees and thickets; (ii) they may be drained and planted. They offer, as they stand, wretched conditions for tree-growth, but particular species, forming thicket, are giving great promise in an experiment in Shinyanga, on which *see* p. 319 below; and one of these, Ceara rubber (*Manihot Glaziovii*), spreads very readily. (iii) The margins of some may be settled. This, however, may add somewhat to the difficulty of excluding fires. (iv) The food animals of the flies may be excluded from the hard-pan strips during the tsetse's season of stress. Experiments on these lines are proceeding already or are about to be initiated.

7.—ATTACK ON *G. MORSITANS* BY NOT BURNING THE GRASS FOR SOME YEARS.

(a) Introductory.

There are, for this purpose, three types of *morsitans* country. In one, on fair soil or under a good rainfall with consequent deeper decomposition of the rock and no formation of hard-pan, grasses, and shrubs can compete with

the grasping miombo (*Isoberlinia–Brachystegia*) trees, and exclusion of fire does often produce thicket (pl. 11, figs. 1 to 6; and Swynnerton, 1921, pl. 17, fig. 2, and 1934, pl. 14, fig. 2); the Kahama–Biharamulo, and Kilosa–Handeni belts are most promising. Wooding of *Ostryoderris Stuhlmannii* and other spp. as a habitat for *G. morsitans* (in Nzega) comes into the same category. In another type (Central Province, Tanganyika), with small rainfall, there is little grass or woody regeneration on the poor, grey, sandy soil and little prospect of producing an early alteration under the actual miombo wooding. This, by refusing to tolerate competition for a too scanty food supply, has in places apparently assumed the rôle of vegetational climax, instead of remaining, as in many parts it certainly is, a sub-climax dependent on the continuance of the grass fires. The *Copaifera mopane* wooding of the Rhodesias also comes into the intolerant category. In a third category, which is more generally prevalent than either and which covers most of the Western Province in Tanganyika, the conditions are varyingly intermediate.

(b) An experiment at Itundwe in the Kondoa-Irangi District.

Here the *Isoberlinia-Brachystegia* wooding is one of the types referred to above as intermediate. A small piece of this country, one and a third miles long by a third of a mile broad, was demarcated for experiment by St. Clair-Thompson, our Forest Botanist, in 1929, and, except for a control plot within it, has been kept unburned since; it has thus missed five burnings. Near it is a further small piece of country that each year has been burned rather patchily and last year was burned not at all. The protected area has thickened up greatly and remarkably early, except at its northern end, and the density of the woody vegetation resulting (except there) is such as in our general experience is unfavourable to *G. morsitans* in the wet season particularly, although it is less than dense thicket (see pl. 11, figs. 1 to 6). The patchily burned country has thickened up also, but less evenly.

The shrub that has produced most of the densification between the trees is a large, woody *Indigofera* (*I. gyrocarpa* Baker fil.). . An *Acalypha* has formed a few dense steadily extending clumps. In parts close stands of *Combretum Zeyheri* and *C. apiculatum* or of *Isoberlinia globiflora* saplings themselves are providing a most useful effect. An unburned piece of open mbuga, also protected by St. Clair-Thompson and representing a feeding-ground of the fly, has densified sufficiently satisfactorily, *Dichrostachys glomerata* being mainly responsible.

Fly work carried out here by Jackson in 1934 produced three times the number of flies per hour of progressive reconnaissance from the regularly burned and undensified *Isoberlinia–Brachystegia* than from the unburned and patchily burned area. They were practically all males in each case owing to the absence of hunger. An organised pupa-search with half a dozen skilled natives produced, per hour, eleven times more live pupae, and eight times more live pupae and old shells combined, from the regularly burned ground than from the country which had densified through not being burned at all. The large corner of the latter which had not densified and the regularly burned control showed approximately the same fly density as the general, regularly burned country. The bad corner, separately searched, showed also approximately the same high pupal density as the latter.

The difference in the number of flies was in spite of the fact that, there being no sort of a barrier between, there must be a strong and continuous infiltration by them into so narrow a piece of unburned ground, and the further fact that

the dry-season conditions and advanced leaf-fall should have been making the thicket country relatively more attractive.

(c) Limitations of the measure.

In the plots laid out by J. D. Scott under J. F. V. Phillips at Kikore, probably through conditions being damper than at Itundwe, non-burning has repressed the growth of the young *Isoberlinia* and other savanna trees, and thicket species, though flourishing, are not present yet in quantity. The presence of the large corner which has failed to thicken up at Itundwe and the position as regards the tsetse within it, together with the results obtained in Kikore, confirm the expectation that there will be pieces of country, whether they be mere patches or complete fly belts, to which supplementary or quite different measures will have to be applied no matter how successful not burning may be elsewhere, or which will require to be isolated from the area not burned. A possible supplementary measure for such places is that of assisted densification of the wooding by the planting at intervals of nuclei of a fast-growing, close-growing shrub or tree that has proved its ability to spread under the conditions involved and form thicket.

The *Indigofera* itself may prove excellent in miombo. Unfortunately a small larva eats its seeds wholesale. An exotic plant might for long avoid enemies. *Tecoma stans* and Ceara rubber (*Manihot Glaziovii*) spread rapidly and form thicket and the young plants of both are tolerant of canopy. Guavas (*Psidium* spp.) might form thicket in Kikore and Handeni as readily as in parts of Rhodesia. The rubber is favoured at present as a first-rate self-spreader, which suits also the difficult hard-pans of *G. swynnertoni* if these are drained, but two conifers—*Cupressus arizonica* and *Callitris robusta*—have done excellently, despite intentional neglect, in our considerable experimental plantings on the ground at Itundwe which refuses to densify, so that where this is economically feasible and the climate is favourable, plantings of useful conifers might form the best supplementary measure. " The planting of vleis and their margins with the heavy wooding avoided by *G. morsitans* . . . to check desiccation, introduce shade conditions inimical to the fly and spoil the game's early grazing " (Swynnerton, 1921 : 377).

An alternative supplementary measure might take the form of an annual exclusion of game in the flies' hungry months, as suggested for *G. swynnertoni*. Or (as an experiment suggests) a modicum of clearing might be of use as in Shinyangà. In the latter place the flies by no means continue to survive in all parts of the hard-pan.

8.—THE EFFECT ON *G. PALLIDIPES*, *G. BREVIPALPIS*, AND *G. AUSTENI*, OF NOT BURNING THE GRASS FOR SOME YEARS.

The reaction of *G. pallidipes*, as distinguished from that of its habitat, is still uncertain, but so far has been promising under Shinyanga conditions; though the new conditions at Itundwe look as though they would favour this fly. In Block 4A at Shinyanga its density fell during our omission to burn from 1929 to 1933, though not so heavily as that of *G. swynnertoni*. In the very dry season of 1934 it rose strongly, not only in Block 4A, but in the control area also.

G. brevipalpis and *G. austeni* are definitely likely to be favoured at first by the effect of not burning the grass and (subject to the results of projected experiment) it may be that the measure cannot be carried out in their neighbourhood, but what has been said of it under each should be consulted.

9.—THE PRACTICAL APPLICATION OF OMISSION TO BURN THE GRASS, IF SUCCESSFUL; AND THE DIFFICULTIES.

A portion of a fly belt might be attacked, or with sufficient organisation a whole fly belt at once. In the former case the unburned strip would be a considerable number of miles wide to prevent possible passage by small numbers of flies, and its fire-breaks might move progressively forward. It would be replaced at a safe number of miles behind with as much burning as might be desired for the restoration of pasture, and the diminishing area of infestation ahead would also each year be burned to attract the flies into itself. Even if a large proportion of the pasture went to dense thicket, additional counter-balancing advantages would have been gained from the annual deposition of humus which would not be burned off and from the lessening of run-off and erosion and the possible improvement thereby of the waters; the area would be regarded as an agricultural reserve and the introduction of settlers when the tsetses were finished would gradually but automatically re-provide grazing. The natural regeneration of useful timber trees, such as *Pterocarpus* spp. (Mninga), *Afrormosia angolensis* (Mwhanga), and *Afzelia quanzensis* (Mkola), would also have been protected.

It may be objected that with the whole country like tinder it will be impossible to exclude grass fires either generally or continuously. Certainly there will be losses, in the first year especially, as there were in Shinyanga when we first controlled fire over a very great area; but the effort in each locality might be needed for a few years only, and our experience suggests that, while trouble may be expected initially and local set-backs for ever, good organisation on the Shinyanga lines with the use of sufficient fire-breaks will see the measure through as a general success—provided that the Government adopting it and the Administration of the district concerned with it are completely determined about it.

A possible source of trouble might be that the smothering effect obtained in the first few years may disappear later if the grass becomes killed by it, and that an intermediate period may thus occur which will be more favourable to the tsetse.

10.—ATTACK BY DISCRIMINATIVE OMISSION TO BURN THE GRASS.

It would seem perfectly possible that densification of the feeding-grounds and their immediate woodland surroundings only, of *G. morsitans*, or its concentration grounds only, may in some types of country serve to eliminate the flies. In the Kahama–Biharamulo belt and again from Kilosa to Handeni and even in South Tabora these sites are for the most part characterised by long grass and are rendered suitable for the flies by the annual burning of the grass. In the Tabora country seasonal or permanent concentration is so marked that the measure will be well worth trying there. In practice the distance apart of the concentration sites would decide the treatment. If some miles apart, separate protection might be best; if nearer, it might be easier to preserve the whole country from burning. Experiments are projected. The concentrations of *G. swynnertoni* are generally too close together for this type of treatment.

11.—ATTACK BY BURNING THE GRASS EARLY.

During fifteen years on a farm in Rhodesia I burned annually some savanna-wooded areas late, some not at all, and some early.

The early-burned areas thickened up very greatly, although less rapidly than those not burned at all.

" Keep the fires from such a piece of ground—or burn too soon—for several years, and these shoots grow up and eventually in places become so dense as to reduce the grass and the severity of the fires and to allow such semi-forest types as *Markhamia lanata* and *Albizzia chirindensis* to spring up amongst them, as I shall describe below, and eventually to replace them. The result, when this occurs so far from high (rain) forest as not to obtain seeds from it, is a form of dense thicket " (Swynnerton, 1917 : 508, repeated 1921 : 382). " On my own land *Uapaca–Brachystegia* areas burned regularly and more or less late have failed to develop appreciable undergrowth, while areas which, for winter grazing, have been burned irregularly and early, have developed it. The latter areas, which were clean-stemmed when I came here, would now carry *G. brevipalpis*; the former would not. Elsewhere in the irregularly burnt area new coppice wooding has sprung up in open ground from long-suppressed underground stumps and roots and could already shelter *pallidipes* " (*ibid.*, 1921 : 382).

While the ground was thus made suitable for the species of tsetse that haunt at least broken dense growth, it was made as unsuitable for *G. morsitans* and *G. swynnertoni* as ground not burned at all, though at that time this was not realised. It is interesting therefore to note in an article by J. R. Ainslie (1934 : 39) that great areas in the Nigerian Forest Reserves, in which densification has taken place as the result of early burning, have become free from tsetse fly—presumably *G. morsitans submorsitans.*

Early burning is very much simpler than not burning at all, and even if it takes longer to produce its effect, it may be best for areas in which it is specially suitable. On ground burned early each year in Shinyanga the densification tendency has been present but has been very slow. On the other hand, on being protected completely this ground has turned into thicket more promptly than have areas with a history of late burning. Possibly here a few years of early burning (costing nothing) followed by three of non-burning would be the cheapest measure, the difficult period of complete protection being thus limited. But there are types of country in which early burning very definitely will not help. It must be proved by experiment to which types it will apply. Further, while non-burning may not in the long run favour *G. pallidipes*, early burning definitely will, for its result will be a more broken thicket. Further, if non-burning allows scattered fly colonies to survive (*see* pp. 275 and 277 above), early burning will do so more freely.

12.—STUDY OF THE EFFECT OF THE ADVANCEMENT OF THE VEGETATIONAL SUCCESSION BY NOT BURNING ON THE PLANT AND ANIMAL COMMUNITIES GENERALLY.

Blocks 4A and 4B were both photographed in mosaic from the air at the time that the experiment was begun. Both have been divided into squares of 1,000 yards by means of path transects. Using these, Burtt (our Botanist) has now carried out a detailed vegetational survey of both blocks to correlate them with the air photographs and to record the progress made, since burning ceased, of the vegetational succession. He had previously thus mapped Block 10A. A study of the vegetation of Blocks 4A and 4B, with the effect on it of the succession, will be based on his map. The run-off of the rainfall will be measured on burned ground and unburned by means of enclosures and tanks of the type

described by Staples on p. 93 of the report of the Tanganyika Veterinary Department for 1933.

It was impossible until 1935, through shortage of staff and time, to study the effect of the release of the succession on the general animal communities, though incidental observations on the game animals and spoor were always recorded (though inadequately) in the fly rounds. Now, as regards the game, Blunt's survey has taken place and has been followed as a routine measure by daily rounds of all transects of each block by game scouts under the supervision of Harrison. As regards insects, it has been decided to concentrate on the grasshoppers amongst day-moving insects, these constituting a varied and readily accessible group of some economic importance and there being no time to do more. In addition five lamp traps for night-flying insects are being set out on alluvial and eluvial sites in Blocks 4B and 4A respectively and in the five-years-unburned Mantini Road thicket-barrier between them. Mr. E. Burtt, our Botanist's brother, a visitor and himself a trained entomologist, has kindly undertaken the initial organisation of these observations and collections, which a trained native will continue with incidental supervision. While specialist surveys would be necessary to do the work properly, it is expected at least to learn a little of the effect of the changing succession on the composition of the insect population. We have little time for work other than on the tsetse itself, but I felt that it would be a pity to miss altogether such a chance of ascertaining the more general effects of the advancing succession.

13.—DISCRIMINATIVE PLANTING.

In view of our demonstrations of the fundamental importance to *G. swynnertoni* of the hard-pan strips in country like that of Shinyanga and the fact that these strips do not densify rapidly under non-burning of the grass, it is a question whether what has been referred to above as a measure supplementary to the latter, namely planting the hard-pan strips, may not suffice by itself. There is little that will grow on them, but, as stated, Ceara rubber has promised well where planted experimentally. Mr. F. A. Stockdale has suggested in conversation two plants of economic value—tree cassava and pigeon pea—the latter of which tends to break up certain hard-pan types. A margin of the neighbouring eluvial ground kept unburned on either side of the plantings would doubtless assist appreciably as regards the effect on the flies.

14.—UTILISATION OF THE BROWSING BY UNGULATES FOR THE DESTRUCTION OF FLY COVER, AND SUCCESSION AS DIVERTED BY GOATS AND BY ANTELOPES.

(a) Goats.

In 1924 I bought some hundreds of goats and placed them in the strip of fly bush first cleared at Lubaga in Shinyanga, distributing them among the first native settlers. They were watched by Teare and myself and proved a disappointment in this *Acacia–Commiphora* country. Pinnae of the acacias would be daintily nibbled off the shoots, the latter being left, and the goats fed very largely on various herbs growing abundantly in the grass. Their effect on woody regeneration was small.

This was very different from the impression which one gains in various native reserves in which the goats have appeared to have been largely responsible for the failure of the wooding to regenerate and the setting back of the succession. All must depend (*a*) on the nature of the wooding to be kept down and the presence of such a herbaceous " buffer " as was seen to protect it in Shinyanga;

(*b*) on the intensity of the stocking, and (*c*) on whether cattle are present to destroy the herbs and leave only the woody growth to the goats. It is a matter for closer study.

(b) Antelopes.

Following the great epidemic of sleeping sickness which destroyed 200,000 out of 300,000 inhabitants in the region north of Lake Victoria in the early years of this century, those still surviving in the Sesse Islands were moved to the mainland to break their contact, and that of the disease, with the tsetse—*Glossina palpalis*. There were no large carnivora on the Sesse Islands, so that, with the removal of the people, who hunted situtunga antelopes (*Limnotragus spekei*) to such an extent that they kept to the protection of the marshes, the latter increased enormously in numbers. They ate off all vegetation to a level height

FIG. 19.—The effect on the wooding, and on *G. palpalis*, of the removal of checks on the increase of a species of antelope—*Limnotragus s. spekei*, the situtunga of Lake Victoria. No large carnivora were present and the population was removed to break its contact with the sleeping-sickness epidemic of the early years of this century. The situtunga so increased that they destroyed all undergrowth and were making the wooding definitely unsuitable for the tsetses when the natives were brought back.

so that one could obtain a view between stems to considerable distances over the close-cropped sward, and they actually (*a*) destroyed, and (*b*) prevented the formation of the undergrowth over large areas. The detrimental effect on the numbers and distribution of the tsetse was strong. Then, except chiefly on Damba, the people were allowed back, the situtunga, which raided their gardens, were again intensively hunted and took once more to their swamps, the undergrowth grew up afresh and the flies once again increased. As an intermediate stage, before the hunting again became fully effective, the increasing flies followed the situtunga to the gardens and were found at fair distances inland.

Up to this stage the activities of the antelopes were definitely detrimental to the flies and in this respect of benefit to man, but whether they would have ended by exterminating the flies is still open to doubt, for there were a very few species of plants which they definitely did not eat, and three of these, *Teclea nobilis*, *Teclea monophylla* and *Markhamia platycalyx*, were, when I examined

Damba and Bugala with Fiske in 1923, already spreading and forming clumps on the former island, to which natives had not returned.

The first effect of the activities of the situtunga on the vegetation is shown in fig. 19, the second in fig. 20. Man's intervention for the suppression of the *Teclea–Markhamia* clumps while the situtunga were dealing with the rest might have ended in the destruction of the tsetse. As it was, the ultimate effect of the antelopes' activities promised to be the substitution of a type of dense vegetation consisting of a few species only for a very mixed type of forest.

What was apparently a similarly destructive effect on the vegetation by a great game population, albeit with carnivora present, was seen also in Zululand

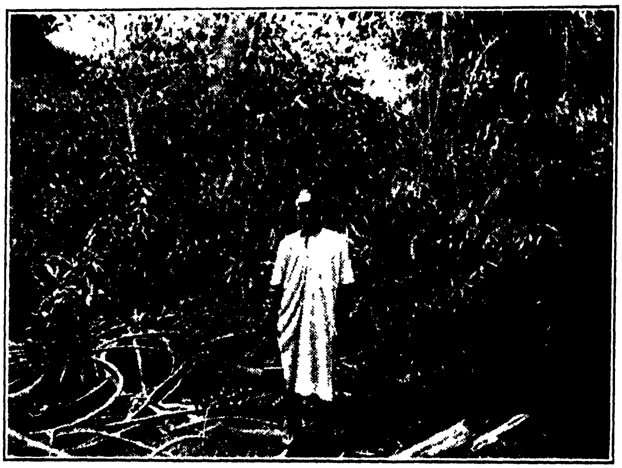


FIG. 20.—A few species of plants not eaten by the situtunga, notably *Markhamia platycalyx* and two species of *Teclea*. This shows the resulting spread of the *Teclea*, which, with the other species that were spared, would doubtless in time have replaced the old mixed wooding.

in part of the Mfolozi Reserve, but, usually, it will be impossible to allow browsing game species so to increase that they will thus " eat out " the tsetse fly without endangering the crops cultivated by the natives, should such be present.

C.—INDIRECT ATTACK ON THE TSETSES THROUGH THEIR FOOD SUPPLY.

1.—DISCUSSION OF THE PROBLEM.

The game helps to feed the fly; it is the reservoir for the infections with which the latter kills domestic animals, and recent experiments (Corson, 1932; Duke, 1935) show that certain species at any rate are capable also of harbouring for two years or more the trypanosomes of Rhodesian sleeping sickness without destroying their pathogenicity for man. It has been argued " if you destroy the game you will eliminate the food supply of the fly and the reservoir of the trypanosomes, and the fly and the trypanosomes will disappear."

Large-scale slaughters of the game have accordingly taken place in more than one country—amounting in one case to 35,000 animals, in another to about 100,000 in all. For one only of these measures, so far as is known, has any full success been claimable as regards its effect on the tsetse. This was R. W. Jack's game measure in Southern Rhodesia, described on pp. 226 and 227 above. In none of these cases, however, was it possible to control the experiment so closely as to be able to say with complete scientific certainty that nothing besides the killing of the game contributed to the reduction of the fly, although it is believed from the general controls available that Jack's experiment had the effect that we deduce from it. Further, as will have been gathered from Part 2, Section P, "the tsetse flies in relation to their food" (p. 195 above), the question is a complicated one. The flies are capable of surviving in numbers in the presence of a very small game population indeed, and they have excellent means of keeping in touch with it when it moves locally; as regards hunger, there is only one relatively brief period of real stress in the year during which serious game absence can harm them, and the flies tend to spread further if they are hungry, a habit that might be disastrous were the game attacked in the wrong type of country. It may be added that the prospect of reducing the game in fairly dense country to the point at which it will not support the fly is exceedingly small, whatever organisation and expenditure may accomplish in more open country, and that each of the many species of tsetse presents a separate problem in connection with food control.

The whole question of the game-fly relation and how far the flies of each species can be attacked through their food supply is of the greatest importance and demands closely controlled experiment, although the method will not, it is hoped, even if successful, be used where there is a practicable alternative. Africa has the unique distinction of continuing to-day to possess one of the most remarkable and interesting faunas that have existed on the earth; its elimination or even its restriction to a few small natural "zoos" before overcrowded development finally demands this last measure, would, in my opinion, be lamentable.

2.—ALTERNATIVE POSSIBILITIES OF ATTACK ON THE TSETSES THROUGH THE GAME WITHOUT EXTERMINATING THE LATTER.

The belief that regularity of habits assists a small game population to feed a large fly population, and that the known disappearance of the fly from the Transvaal before the game went may have been due to disturbance, has suggested as one of our experiments the ascertainment of the effect of keeping the game on the move and making it also nocturnal without seriously attempting to exterminate it. It is noted that Jack's results confirm the importance of this.

The effect of a special effort to keep the game out only during the season of stress of the flies, and only out of the feeding-grounds of the flies, is worth ascertaining also.

Keeping the grass unburned is, as has been stated (pp. 272–278 above), a promising measure against *G. morsitans* and *G. swynnertoni* in country of certain types, but strips and patches of tsetse are left—as, for example, on hard-pan. The exclusion of game from these strips alone during the months July to November in the unburned country has been suggested on p. 277 above.

Tsetses show definite food preferences. Potts's results from the feeding of flies on goat and cheetah have been mentioned already, and it is possible that a fly population might not survive indefinitely were certain animals removed and

others, less suitable, left. Experiments in our zoo at Shinyanga and in the field are planned in this connection.

3.—THE GENERAL EXPERIMENTS PROPOSED.

An experiment will be carried out in the exclusion of game from an isolated *morsitans* fly centre. If possible a well-stocked fly concentration with pig and buffalo will be chosen. These will be banished first and the whole effect noted.

The experiments started in Shinyanga in connection with *G. swynnertoni* (*see* sub-section 4 immediately below) will be continued.

An experiment will be planned later for an isolated and typically thicketed area combining *G. pallidipes*, *G. brevipalpis*, and *G. austeni*.

As a finish to our experiments on *G. palpalis* on Maboko Island, if flies are still present, the same will be done locally as regards crocodiles and, later, monitor lizards.

4.—THE EXPERIMENTS AT SHINYANGA TO TEST THE VARIOUS POSSIBILITIES.

Block 9, with an area of 55 square miles surrounded on three sides by closely settled country, partly separated on the fourth side and easily separable entirely, has for many years been reserved for an ultimate game experiment, but through lack of money and of confidence in the position of our Department, it was only in 1934 that it was decided to make a start. As at least two separated areas are necessary for the trial of the experiments listed below, in addition to game sanctuaries, it has been decided to include in the scheme the whole of Block 10, subdivided. Map 2 should be consulted in this connection.

In Block 9 it is our intention to ascertain the effect on the flies and their infectivity (i) of making the game irregular in its habits and nocturnal (α) only in the season of stress for the flies and in the flies' feeding-grounds, and (β) more generally; (ii) of various degrees of reduction of game if (i) does not suffice; (iii) of expulsion of game, in so far as this is possible in a block of this size.

In a small (western) section of 10B it is hoped to ascertain the effect of the successive removal of the game strata. As now roughly intended, first the large animals of relatively stationary habits would be removed, then those of the size of impala, reedbuck, and duiker, then the dikdiks. Possibly the pigs (wart-hog and bush-pig) last, as it is doubtful if these form an important reservoir for the trypanosomes. One might find tsetses surviving in numbers but uninfected. What animals are first removed and what left will in any case depend on the result of our preference experiments on the flies (*see* pp. 200–202 above) and our field observations. Thus our giraffes are wide in their movements, never staying long even in the big Block 9, and the elands are occasional in their visits. Both might be left out.

In Blocks 4A and 11 it is proposed to carry out the small but highly important experiment of keeping game out of the feeding-grounds only at the season when conditions are hard for the flies.

The general experiment is designed to take place over as large an extent of country as is felt to be compatible with good observation, in order to simulate as nearly as we can the conditions that would actually confront us in a given practical problem. It would be completely useless to banish all the ungulates from three or four or a dozen square miles of country. This might almost be possible, but the inference, if the flies disappeared, would be purely academic.

To obtain really practical conditions, it would have been preferable to have had Block 9 much larger still.

5.—THE DETAILED SCHEME FOR SHINYANGA.

(a) The work initially planned.

The work initially planned included :—

(i) The sub-division of each block into squares as described on p. 30 above, under Botanical Survey, by means of narrowly hoed transect paths.

While this introduces a not quite natural element in the shape of paths which the game will use, it was felt that it would not be serious, as game-paths and man-paths exist in the bush in any case. It was certain that without this visible grid it would be impossible in such large, flat, pieces of undifferentiable bush country to make a detailed botanical map or to observe and record accurately the movements of the animals and of marked flies. As it is necessary for the natives employed to know and to refer to the squares it has been found better to use for each the combination of a letter and a number rather than line co-ordinates. Thus in Block 10 A the squares from north to south are lettered from A to J and the squares running west from the north-south road on the east are numbered from 1 to 6 (*see* fig. 7).

(ii) a detailed botanical map of the whole of each block, with a view to taking into the fullest account the vegetational basis of the distribution and movements of the vertebrates and the flies.

Soils and the geological substratum to be noted as well, and waters, seasonal and permanent.

(iii) as close a game survey as possible, the different herds, parties, pairs and solitary individuals being so far as possible differentiated, the survey of the small mammals by means of sample trapping.

Bat colonies in hollow trees to be investigated. The incidence and influence of direct and indirect tsetse enemies to be noted if at all possible.

(iv) a survey of the detailed density-distribution of the tsetses, *G. swynnertoni* (abundant) and *G. pallidipes* (sparse).

Screens and traps to be used to elicit information on the latter.

(b) Intermediate work, to last, if necessary, for two years in order to obtain as thorough a preliminary knowledge as possible of the inter-relations of the flies, the undisturbed game, the vegetation, and waters.

The intermediate work was to consist as follows :—

(i) Regular reconnaissances and rounds, by game scouts, fly boys and the officer-in-charge, in order to keep in the closest touch with the density, movements, and habits generally of all observable local food animals of the tsetse and of the flies themselves;

(ii) a study of the preferences of the flies and the effects of the different bloods;

(iii) the ascertainment by the precipitin and corpuscle-measurement tests, as well as by direct observation, of what animals the flies are most feeding on;

(iv) examination of the flies to ascertain their trypanosome infections and

the incidence of the latter through the year and if possible in different sub-localities;

(v) broad phenological observations of dates of leaf-fall and flush, grass-conditions, etc., and their effect on vertebrates and fly;

(vi) regular meteorological observations, including special comparative observations of the physical conditions in the main vegetation-sites that should prove of importance in one way or another.

(c) The final experiments.

The final experiment will consist in the harrying in Block 9, the progressive elimination of species in Block 10B, and the smaller experiments in the hard-pans of Blocks 4A and 11, that have been referred to already, the observations of the intermediate period still continuing steadily throughout.

An examination of stomachs will be carried out during the shooting period for more light on the feeding-habits of the animals. Meantime direct observations are being made of their feeding. Infections and parasites of the various animals will be noted when the time comes.

(d) Sanctuaries.

The blocks between the main experiments, namely Blocks 10A and 10C, will be sanctuaries; Block 10C will be extended half-way across Block 10B, a new dividing clearing being made, and both it and Block 10A will be provided with water and other amenities for the attraction and retention of game. The amenities will be the subject of study in relation to the requirements of the several species to be accommodated. A combination of riverine thicket, eluvial savanna wooding, and succulents for the kudus, of open country for the impala and other game to resort to in the evenings or when pestered by flies or lions, additional *Harrisonia* (or even a cotton field!) for green stuff in the dry season, and salt for all species, are likely to be amongst these. Block 10A will be unburned; Block 10C will be subject to ordinary native burning. It will be seen if the large influx of game to be expected into Block 10A will nullify the effect of not burning.

(e) The barriers round the game experiments.

It is proposed to try to ascertain incidentally (i) to what depth into Block 9 the flies will return at different seasons if the game is kept out by a fence, but no fly barrier beyond the incomplete barriers already existing is placed in the way of the tsetses; and (ii) the effect of the game expulsion in the same blocks when surrounded by good game and fly barriers. One such barrier will be carved out of Block 9 itself and the other will surround Block 10B.

(f) An experiment in the trapping-out of the flies in one of the sanctuaries.

An experiment of this kind will be undertaken in Block 10C if and when the game becomes really abundant there.

(g) The organisation of the work.

Harrison, who has great experience of game, and whose exceptional qualifications for the task have been mentioned on p. 24 above, is in charge. Native game-scouts are assisting him with the game observations and work, and trained fly boys with the fly work. Abdu Charamanda, ex-K.A.R. sergeant, later a game-scout, who followed me when I left the Game Department, is Head Scout.

Mr. Symes, Medical Entomologist, Kenya, has kindly undertaken the precipitin tests, and Potts, at Shinyanga, will carry out the preference and food-value experiments and examine for trypanosomes. Dr. J. F. Corson, our neighbour in charge of the Trypanosomiasis Research Laboratory at Tinde, has also kindly offered us his assistance—an offer that will be gratefully accepted.

This organisation will not suffice to see the experiment through even its initial and intermediate stages, nor can it continue without extra funds; but the experiment having already been far too long postponed through shortage and uncertainty of funds, I decided to start it in the hope that the latter might materialise. Even its first two stages should provide a valuable ecological study of certain species of game animals and of game-fly relations.

6.—WORK ACCOMPLISHED IN THE FIRST YEAR (1934).

(a) Work in Block 10A.

This is a game sanctuary with no grass-burning, 1934 being the third year in which fire was excluded.

(i) *Preliminary survey.*

This block was photographed in mosaic from the air in January 1932. Being small ($2\frac{1}{2}$ square miles) it has been cut into squares measuring only 500 yards each way and a detailed botanical map of the whole of it was made by Burtt in January 1934.

(ii) *Observations.*

Game rounds and fly rounds were started in this block by Harrison in March 1934 and have continued regularly since with interesting results. Some details have been given already on pp. 43 and 47 above. With a considerable under-allowance for dikdiks at least, it is computed that the animals seen during December 1934 averaged 63·20 per 10,000 yards of transect, or 74·68 per square mile. The fly round, which traverses a large proportion of the block and typical samples of all the vegetational types, is carried out twice a week. On one round weekly the flies are killed for examination, on the other they are marked with distinctive dots of oil-paint in order that their subsequent movements may be noted (*see* pl. 21).

(iii) *Provision of attractions to game.*

Much new thicket in Block 10A (and along the south margin of Block 10C) produced by not burning the grass, for species that specially use it, has been provided already. An "earth water-tank" (*see* p. 422 below and pl. 16, figs. 1 and 4) has been excavated. It filled with the last rain of 1933–34, held water till September, and would have lasted throughout the season, if its water had not had to be taken by a large labour gang excavating tanks for cattle outside the block. The division between Blocks 10B and 10C will be shifted much to the west, so that the present clearing between them, open but for the runways of bush that have been left uncleared on the streams (*see* map 2), will be in the middle of the Block 10C sanctuary to give the game animals the open element that even kudu will use.

(b) Work in Block 9.

(i) *Preliminary survey.*

An air reconnaissance was first carried out, by Burtt and myself in December 1933. The old German road, which cuts the block diagonally, was re-opened

and the laying out and cutting of the transects undertaken and completed. This work took Harrison three months, during a few weeks of which he was helped by Lombard. He has since carried out the vegetation survey and mapping of two-thirds of the block. This he has accomplished in great detail with prismatic compass and measuring wheel; almost every little thicket has been mapped in as well as the larger areas of each vegetational community. One square is shown in fig. 5. The plant species in each community have been listed and their broad relation with the edaphic conditions has been noted.

(ii) *Observations on the flies.*

A fly round in the west of the block, opposite Block 10 A, was started in March 1935, and others have been added till five are now regularly carried out. Round no. 4 was specially devised to intercept the south to north game movement to water referred to below, and has shown that whereas flies were practically absent from the north end of the block before the movement began, they had by October become very numerous there and quite well fed, while the flies in the south of the block had somewhat diminished.

(iii) *Observations on the game.*

Game rounds were started in June 1934 and at the time of writing the present paper (1935) no less than twenty such rounds in all blocks taken together were being carried out regularly. Every yard of the 140,800 yards (eighty miles) of transect is (as stated under "technique," on p. 43 above) traversed once in three days. Each scout carries a plan of the block and a form on which the observations for that day and the square to which each refers are entered. Harrison enters the daily position of each herd on maps which cover a month, and by connecting these daily positions, using for each herd a line of a particular colour, he is able to see at a glance its movements through each month (*see* fig. 7).

The preferences for, and special use made of, different categories of country by each species at different seasons and under different conditions is being studied. In addition the animals are watched feeding, and a monthly list of the plants eaten is compiled for the various species. A paper by Harrison which will be published in " Animal Ecology " will contain further information about this. *Harrisonia abyssinica, Elaeodendron Stuhlmannii,* and tamarind (*T. indica*), all relatively neglected in the rains, are greatly eaten by most of the animals in the dry season owing to their long retention of leaf. Harrison has been supplied with a particularly fine pair of field-glasses, and it is hoped that he will also be able to make many notes on the feeding of tsetse on game when the time-devouring vegetation survey is finished.

A rain-gauge has been installed in Block 9; otherwise the readings at the Old Shinyanga open station, a mile and a half from the south of the block, are being used for the present. When these were tested against a set of instruments placed in Block 9 during previous fly-trapping experiments, it was found that there was a regular and fairly close correlation between the two sets of readings.

(iv) *The preference experiments.*

The beginning of the experiments in the feeding value for tsetse of the different animals is in progress and is in the hands of the Senior Entomologist. It has been touched on already on p. 284 above.

(v) *Some initial results.*

Considerable difference can already be seen in the ranging of the different herds even of a single species, and it is hoped, by study and comparison, to arrive at a knowledge of the animals' requirements through the year. Already a great deal of information has been collected on the composition and movements of the individual herds, sounders, parties, troops, pairs, and some individuals of each of the following species : giraffe (*Giraffa camelopardalis tippelskirschi* Matschie), greater kudu (*Strepsiceros strepsiceros bea* Heller), eland (*Taurotragus oryx pattersonianus* Lyd.), roan antelope (*Hippotragus equinus langheldi* Matschie), impala (*Aepyceros melampus suara* Matschie), savanna duiker (*Sylvicapra grimmia* Gray), steinbuck (*Raphicerus campestris neumanni* Matschie), dikdik (*Rhynchotagus kirki cavendishi* Thos.), zebra (*Equus quagga granti* de Winton), wart-hog (*Phacochoerus aethiopicus* Pall.), baboon and black-faced vervet monkey (*Cercopithecus aethiops* Linn.). Thus there are close on 800 impala in the block, varying from a single individual to a herd of 21; four present herds of 2, 4, 8, and 18 are composed solely of males. There are normally about 80 giraffe, but this number has been increased by immigration on two occasions to 142 and 147, and considerable interchange and movement takes place normally, even the 80 not being present all the time. The following were the totals of giraffe seen on two days in four blocks :—

TABLE 50.

The number of giraffes seen on two days in four experimental Blocks in Shinyanga.

Block	Square miles	January 9th, 1935; giraffes seen	Giraffes seen per sq. mile	January 15th, giraffes seen	Giraffes per square mile
9	55	142	2·58	147	2·67
10A	2	9	4·50	28	14·0
4A	4	23	5·75	7	1·75
4B	1·75	1	0·57	53	30·28
Totals	62·75	175	2·78	235	3·74

The number of giraffes on these two occasions averaged 10·08 and 10·44 respectively per 10,000 yards of transect in Block 9 (140,800 yards) and 3·74 and 11·54 per 10,000 yards in Block 10A (24,050 yards).

The total number of the more conspicuous species of animals definitely known to be in Block 9 was, in December 1934, 1,340 or 95 per 10,000 yards, or approximately 27 per square of 2,000 yards, or 24 per square mile. This excludes duikers, steinbucks, dikdiks, and hares, of the populations of which animals only a small proportion can be seen on the transect rounds.

Harrison made a dikdik count for four typical squares, by driving, with the following results :—

(α) 144 dikdiks were flushed in the four squares, the average combined count from the transects of which had so far been 12, which gives us the provisional ratio of 1 : 12 for use on the transect work. The first month (Jan. 1935) for which this ratio has been tested on animals actually seen gives an estimate of 1,350 dikdiks for the whole block. Allowing for half squares on the margins, 1,728 is the figure that we should have expected if the four squares

had been typical of the rest. It is probable that when we check the estimate after burning, larger numbers will be detected.

(β) It was noted that the more eluvial was the ground, and particularly the more *Abrus Schimperi* shrub-cover was present, the more numerous were the dikdiks; the figures for the four squares were 47, 36, 32, and 29 respectively, and the *Abrus* area of each was found to be roughly proportional.

(γ) " Edge-effect " (Leopold) or " concurrence of requirements " (Swynnerton—see definitions) as regards contact of thicket with savanna wooding was, and commonly is, strongly noted for the dikdiks. They are also often specially numerous where thickets abut on quite open ground.

Harrison has already with his glasses watched the flies feeding on giraffe on two occasions, on the fore-legs and chest, and has obtained other observations definitely connecting tsetse flies with the giraffe. Observation of zebra at 40 yards range on very numerous occasions with the glasses has so far failed to reveal tsetse.

Much information has been obtained on the movements of the various species to water. The greater kudu and dikdiks appear to be completely independent of it and make no effort to obtain it. Their distribution in the dry season seems dependent on considerations of shelter and food only, though the latter no doubt includes water-containing plants, such as *Sanseviera* spp. and *Euphorbia Tirucalli.* The impala have been watched chewing *Sanseviera.* The giraffes and zebra, and some of the impala herds and sounders of wart-hog, work to and from water outside the block to the north. The roan antelopes, other herds of impala, and other sounders of wart-hog work to and from a water on the east. The baboons and vervet monkeys have moved in from the east to our earth-tanks in Blocks 10A and 10C, which were used also by our one rhinoceros (now dead), one party of giraffes and the carnivores. Elands were beginning to use the tank in Block 10C and birds—such as sand-grouse and black-winged stilts—are also being attracted. These waters will probably become more generally used, as is the tank in Block 4B, when their white earth banks become grassed, but Blocks 9 and 10B are in the meantime being given temporary tanks of their own.

Other game observations also have begun to be made, but the fuller development of these must await the close of the vegetational survey. Thus the preying on dikdiks by the martial hawk eagle (*Eutolmaetus bellicosus*) has been noted both by Harrison and (in Block 11) by Vicars-Harris. Harrison has also noted that a broad " cotton-soil " mbuga may be something of a barrier to dikdiks. One was watched crossing a quite narrow mbuga with widely-cracked soil with great caution and obvious difficulty, though impala cross it with assurance. November to the end of May has been the calving season inclusive for the antelopes generally and giraffe, and the season 1934–35 was an exceptionally good one. It has been noted that the greater kudu after calving keep to dense cover till the fawns have gained strength, then again use the savanna and open for feeding. Many other observations have been made, some of which will figure in Harrison's paper.

In the sanctuaries (Blocks 10A and 10C) the open hard-pans appear of particular importance to giraffe and zebra; the riverine thicket to the kudu. Eland find most of their browsing on the eluvial, which also the greater kudu use much and the dikdiks definitely require.

The effect of not burning the grass and the production thereby of much thicket is already to be noted in a remarkable increase in the numbers of bush-buck, *Tragelaphus scriptus* Pall. ssp., and bush-pig, *Potamochoerus koiropotamus*

prob. *daimonis* Major (both hardly known in Shinyanga before) and of greater kudu (of which a few years ago there were very few). No less than 36 kudu were counted in a single day, of which approximately 20 base themselves on the densified areas of Block 4A. Excellent litters of the bush-pigs—one of ten and one of six have been noted—promise further increase here too. Bushbuck kids are also in evidence. The bush-pigs may need control, but generally the testimony to the effect of our incipient game management is exceedingly interesting and gratifying, and it gives us the beginnings of experimental evidence on the needs of the species and on the reasons for the limitation in their distribution.

Definite hydroseres have been initiated in the margins of the " earth tanks." Even bulrushes are in some cases present already and the bird population is affected. Stilts (*Himantopus himantopus*)—mentioned already—and sandpipers are regularly present; great numbers of birds, doves especially, come to drink, and wild life generally shows signs of concentration on some of the waters recently supplied.

In this connection may be mentioned an interesting point which arose during Lloyd's observations on Riamugasire Island. This was that his crocodiles were not scared appreciably by noises. If any movements were made during his observations on rocks in the lake, the crocodiles were off like a shot. However, at the close of a day, when the canoe boys were called to remove the entomologist from the rock, loud shouts had no effect on the crocodiles.

(vi) *Setbacks to the work.*

The natives towards the close of the dry season drove their cattle by the thousand to graze into, and across, the block, in the very thick of the tsetse, where many of them died in consequence, rather than take them a dozen miles further to graze on the north-western plains. It was many weeks before this was remedied and the observations were severely interfered with meantime.

A second disaster occurred in the shape of the loss of " Lucy," Harrison's only rhinoceros. After staying contentedly for months in Block 9 and not worrying anybody she conceived the idea one day of exploring the great cultivation steppe to the east of it. She was at once surrounded by a horde of howling natives who, keeping at a safe distance, drove her further and further into the settlements, until she was finally done to death by an Arab. The loss has been a great one, for our only other " rhinos " (black rhinoceros—*Diceros bicornis* L.) are three which confine themselves to the furthest parts of Block 11 and are not accessible for close observation.

The whole experiment is expected to last eight years, and a difficulty before then may be the encroachment of the native population which inevitably takes place as soon as flies become sparse. We shall have to be insured against this and against repetition of this year's invasion by cattle, or it will be better even now to transfer the work to a new site.

D.—INDIRECT ATTACK ON *G. MORSITANS* BY THE INTRODUCTION OF HUMAN ACTIVITIES.

The apparent repellent effect on *G. morsitans* (but not on *G. swynnertoni* or *G. pallidipes*) of intensive human activity is dealt with in part on p. 325 below in Part 4, Section E, under the heading " human activities as a fly barrier." The qualifications may be usefully stated here.

In the first place it is doubtful if this should have come under a separate

head from that of "attack by discriminative settlement," on p. 270 above; for, whatever the repellent effect of human activities on *G. morsitans*, it is certain that this cannot be vital unless they are situated at its primary foci (see definition of "focus" in appendix 1) or across its communications leading thence. It is to be noted that Lamborn's settlements flank each side of a great "dambo" or mbuga, of a kind that would certainly have become a primary focus for the flies, that stretched across their advance and, if settlement had not occupied it first, would have given them splendid conditions for increase and further advance. To recognise all the primary foci, actual and potential, and at the same time not to waste settlers on the secondary ones that do not matter, needs expert knowledge and investigation.

Secondly, if we should (let us say) supply water and other attractions at all the primary foci in an area infested with tsetse and then leave it to the natives to occupy them, and so, possibly, drive out the flies, we should be disappointed. It must be remembered that they must occupy them all and in sufficient numbers simultaneously, if they are (*a*) not to create a dangerous position as regards sleeping sickness, and (*b*) to expel the tsetses; and that it is unlikely that this can be brought about except by large-scale compulsory movement such as is used for the control of sleeping sickness.

It was hoped in 1923, when we started our work in Shinyanga, that the voluntary settlement of natives in the infested bush, drawn thither by the water and other attractions that we offered, might itself suffice to push back the tsetse (in that case *G. swynnertoni*). This part of our hope was disappointed, for it was, and has continued to be found, that, except for odd individuals, the pastoral-agricultural tribes that we are dealing with will not voluntarily settle in tsetse-infested wooding unless we first drive the tsetses out. The further fact that whole tribes, with reluctance and grief, are being driven by the tsetse from their ancestral lands, from abundant waters, and from good soil and pasture, under European administration (pp. 424–438 and maps 5 and 6), is further evidence, if such were needed, that the problem even of *G. morsitans* cannot be solved merely through the presence of attractions to man to enter—or remain in—the bush.

But I feel that it would be particularly worth while to undertake an experiment consisting (*a*) in a thorough investigation of the best sites for settlements, from the point of view of controlling the tsetse, (*b*) in their judicious settlement, with water and other aid supplied, and (*c*) in close observation of the result, and of the ways in which the presence of man repels the flies, if it does so. I hope to be allowed to carry out such an experiment.

E.—DIRECT AND INDIRECT ATTACK COMBINED.

(map 2.)

1.—ATTACK BY ORGANISED GRASS BURNING AFTER AN OMISSION TO BURN.

(a) The fire of 1931.

No fire took place in 1930 in Blocks 5 and 11, but Blocks 5A and 5B were burned according to plan; Block 11, through an accident, had unfortunately to be burned in the late afternoon and in consequence only the eastern portion burned well.

Reconnaissances by Jackson and Lloyd showed the following results :—

(i) Immediately after the fire, there were no flies to be found in Block 5A

except one fly in some grass burned prematurely and four in the "new mbuga," the hard-pan of which, with the thickets that its short grass protected, had burned very patchily and into which swarms of other muscids also had been driven;

(ii) A few flies only (11) were found the day after, and these were either on hard-pan or at thickets;

(iii) A complete drive-out of the flies occurred wherever the fire had a clear run;

(iv) Exactly the same fly density was found after the fire as before it in a piece of ground that burned badly, and evidence from marked flies showed that the same individuals still remained there;

(v) The flies passed over a cleared fire-break, whereas they lodged in fire-breaks in which there were trees.

> It is on this observation that we have based our view as to the usefulness of clearing the trees on all patches so poorly grassed that they will not burn well;

(vi) An immediate return of the game was noted in the burned area—roan antelope, duiker, dikdik, giraffe and wart-hog;

(vii) A concentration of game and of fly in considerable grass-patches escaped the fires in Block 11 owing to the late afternoon burning.

> This concentration continued with a mean hunger stage of the flies of 2·7 (well-fed) and a female percentage to man of only 1·1—which denoted "home" conditions with plenty of food. The game and the fly had been brought into the closest of contact, and the tsetses were having "the time of their lives." This obviously happens always in the course of uncontrolled fires which leave many patches unburned.

In general, the flies in Block 5A, already brought low by catching in the feeding-grounds, were further reduced by the fire by about two-thirds. The infestation was thinned greatly in much of the rest of Block 11, but owing to the poor burn beyond, the non-penetration of thickets there by the fire, and there being no barrier between, it recovered its former density here fairly rapidly.

This fire (after an omission to burn in the previous year) was undoubtedly fiercer than the average organised fire, and its effect in destroying acacia trees and burning through thickets was very great (pl. 14, fig. 2). Its effect in Block 11 would certainly have been greater, if it had not been for an accident connected with one of the fire-breaks, and it did actually drive the flies out of the "Chibe" block, not then as yet separated from Block 11, and concentrated those that remained in a few granite kopjes in which they were specially attacked afterwards.

(b) The fire of 1932.

The fire of 1932 was spoiled in Block 5A by one of the natives who lighted before the signal and whose burning was taken as the signal on an unsuitable day, on which it had just been decided to "call off" the fire. In Block 11 it was spoiled completely by the great damage done to the grass by the locusts. The eaten patches, in which the grass had subsequently been completely replaced by small Indigoferas and other non-burning herbs, split the fire into numerous tongues, so that no "drive" effect was obtained.

In the result, flies diminished in all blocks subsequently to the fire but not to the same extent as in 1931. The flies increased in the control block (Block

4B) during this same post-fire period (*see* fig. 10). This control block is purposely burned early and patchily, native fashion.

A repetition of the first accident has been guarded against, but the large-scale activities of locust hoppers and the extermination of tsetses by grass fires are incompatible.

2.—DISCUSSION OF THE WHOLE MEASURE.

Our success in holding up early burning and our technique have both steadily improved. The grass fires were held up for two years in Blocks 5, 10B, and 11, and a fire was put through in 1931. A small portion of Block 11 had been lost. In 1932 not an inch of country was lost to early fires, though much was lost to locusts, which spoiled our burning; the year 1933 was particularly successful as regards protection.

Following early experiments carried out by myself in Rhodesia and a highly promising October experiment in Kilosa, a large-scale fire was lighted in Nzega and Shinyanga on 7th–8th September, 1924.

The position before the fire was that not only the drainage valleys but also the general bush on the well-drained ground was, in Blocks 5 A and 11 especially, full of scattered small thickets which the flies were using and breeding in, as evidenced by the finding therein of numerous puparia, and the fact that the flies were abundant there.

The fire itself was remarkably successful except in Block 7, in which, coming from Nzega late in the day, it became a night fire; in Block 9, the fire in which was kept till too late in the season; and in Block 3, a mistake in the lighting of which caused failure.

" The effect of a drive appeared to have been obtained over a fair proportion of the two large sections that were burned according to plan—Nzega and Mantine. The fly was absent from considerable extents of ground on which it had previously been pestiferous in its attentions, and even a month after the fire it was possible to go over these without attracting a single fly, or attracting, it might be, no more than one or two in the course of a considerable walk. Bait-cattle working over areas in which they could previously count on taking fifty or sixty flies in an hour, or were assailed by more than this number at once, would come back with a total bag of eight, ten or twelve flies for the day. Mr. Teare, reporting on these areas two months after the fire, stated that the flies remained exceedingly scarce.

" Wherever appreciable grassless thickets or thicket-clusters had not been burned through (and there were still, in places, many such), and in a piece of ground burned early in spite of us, flies continued to be present, and in the latter and the more important of the former we found them collected in vastly greater numbers after the fire than before it, having obviously been driven into these places. We had not the material to deal with all these collections, but 19,927 flies were caught in one of the two collections that were dealt with experimentally. In the smaller of the unburned thickets only an occasional fly was found " (Swynnerton, 1925 : 329).

It would be impossible to take anything approaching 19,927 flies in a limited piece of ground after one of our present-day fires, which is evidence of the truly vast difference in the fly population then and now.

Block 1 had been cleared of thicket before the fire except for one patch of thickets accidentally left. Two or three flies were taken in the latter after the fire, but otherwise the block, full of fly before, was clear of fly after the

fire and remained clear, as continued reconnaissances showed, until about two months later, when the tide of flies flowed back in Block 5 opposite, and flies from there re-infested Block 1 across the inadequate clearing. It was re-cleared of fly later by catching.

Block 6 contained few thickets with which the fire itself could not deal. I conducted the members of the East African Commission through this block subsequently to this fire, and only two or three flies were seen, although there were plenty before. It took about three more fires to clear Block 6 for practical purposes, but local re-infestation still took place in the south-west, apparently owing to a herd of eland which daily crossed from Block 7. It ceased when the movement had been stopped by the shooting (finally) of 16 of the animals. Cattle were brought in and have continued there, and the block is being eaten up by settlement, attracted by the absence of fly. Probably small intermittent re-infestation has actually taken place, for the cleared barrier between Blocks 6 and 7 is only half a mile wide and contains settlement. That it should, nevertheless, have been so successful, apparently, is put down by Jackson to the fact that Block 7 is margined by much thicket of a fly-excluding character along its north side, by myself in addition to the fact that with the scattered small thickets of Block 6 so completely destroyed as they were by the fires, discriminative clearing has come about and contributed to keeping the block clear.

The history of Block 5A (fig. 10) has been most interesting and instructive. The fire of 1929 brought its fly numbers down in spectacular fashion without any clearing of thickets, except the very considerable clearing brought about by this and previous fires on its eluvial areas. Hand-catching followed in the hard-pan glades, as has been already described, and this brought the flies to such low numbers that it was thought that a single good fire would easily drive out the survivors. This did not happen. In the main wooding a fly could rarely be found, but a few surviviors clung to the thickets and trees of the hard-pan concentration grounds in which, through poverty of grass, the fire is always ineffectual. Most of the thickets in these were cleared—a measure which elsewhere had sufficed; but here some flies still clung, and thus afforded an excellent illustration of the fact that the habit of concentration in tsetse flies enables the sexes to meet and continue their kind even when reduced to very small numbers indeed. It is true that in this case the situation was complicated by the dribble of reinforcement that came in all the time (as marking experiments proved) from Block 11, across an inadequate barrier of 800 yards (pl. 18, fig. 1). It was complicated further by the fact that the natives, owing to the block being to all appearance clear of fly, rushed into it the starving cattle from their grassless cultivation steppes and thus provided the surviving flies with plenty of food and (by grazing) the openness of ground everywhere which the flies love and which prevented further burning. In addition, many of the new settlers in Block 5A went to and fro to water-holes in Block 11 and large numbers of flies had been carried in by them before this movement was discovered. In 1934 appreciable new infestation had taken place.

The last step was the clearing of the scattered trees of the concentration grounds as well as such thicket as was left. It was notable that where this was already done the flies had not recovered the ground, and it is notable now that with the extension of the measure the distribution and numbers of the flies have become negligible once more.

Further sub-problems associated with the firing measures that have been discovered and solved by the large-scale field-experiment method have been the

best methods and organisation for preventing and dealing with premature fires, and for carrying out the burning. The types of country in which burning is useful and useless have been ascertained also.

Actually it was realised from the 1921 experiment in Kilosa that thickets which the fire would not burn through would have to be cleared. After the first (1924) experiment in Shinyanga, I wrote " it would appear from all the results obtained that we may find late grass burning to be a really useful measure, if carried out in suitable weather and if thoroughly well organised and combined with a previous destruction of all possible thickets of any extent. . . ." (Swynnerton, 1925 : 333). It was remarked in 1924 from the site of some of the concentrations after burning that ill-grassed mbuga would need to be dealt with, and it was found in 1932 that instead of catching-out at these the strips could be cleared of trees. The granite kopjes were also experimentally cleared before the next fire, with excellent result. It was revealed also from the limited effect of the " two-year " fire on the uncleared hard-pan patches of Block 5A that even in connection with such a fire, fiercer and more effective generally than a one-year fire, discriminative clearing would usually be necessary, though there were cases in which we had cleared the flies out by fire without this.

The original measure of late, organised grass burning, is now therefore combined with the clearing of thickets and trees in the feeding-grounds. It will have been seen above (in the section on discriminative clearing, on p. 268) that an experiment in clearing on these lines in the Outer Circle also has been very successful but that it has given rise to the question " will not this amount of clearing get rid of the flies without late, organised, grass burning ? "

PART 4.—OBSERVATION AND EXPERIMENTATION DIRECTED TO THE PRODUCTION OF AN ABSOLUTE FLY BARRIER.

A.—INTRODUCTORY.

Shinyanga, the site of the live game-fence experiments and of the planted-thicket experiments against *G. swynnertoni*, suffers from a particularly severe and trying short dry season and many long furnace-like gaps between thunder-showers during the rains. The soils, though largely good, are exceedingly shallow, drying out and heating up with rapidity, and the concreted hard-pan which underlies them and produces this effect often comes out on the surface. This general combination makes it a very difficult matter to get trees and shrubs safely started, and the termites are exceptionally bad. In the long dry season, again, evaporation rates reach a height unknown to our stations in Kondoa, and plants have to be specially drought-resistant and particularly well established to survive. In addition, the rains of the last three seasons have been very broken and defective. At our *morsitans* planting station, Itundwe, in Kondoa–Irangi, both moisture and soil-depth conditions are a good deal more favourable and results from planting have been more easily come by.

B.—INVASIONS OF COUNTRY BY THE TSETSES.

1.—THE MEANS OF DISPERSAL OF THE TSETSES AND THE MECHANISM OF THEIR INVASIONS.

(a) Carriage by trains and cars.

Female flies as well as males travel in immense numbers on cars and on trains. When the Shinyanga–Mwanza road ran through a fly belt, flies (*G. swynnertoni*) were carried in fifties and hundreds to forty miles and more into the open country to the north by numerous lorries and cars daily. A tsetse (*G. morsitans*) was recognised by Burtt on a train in Dodoma station nearly a hundred miles from the nearest fly belt, and he considers that he has evidence for the view that the relatively recent and isolated Hika fly belt in Manyoni, which he investigated, was created by the daily immigration into new country of great numbers of flies (*G. morsitans*) on the trains. The number of flies which it takes to found a new colony under favourable conditions is unknown : it would seem from other evidence to be considerable; but railroads and motor roads passing from actual fly country into potential fly country are at least a very great danger.

(b) Carriage by man and on man's paths.

An occasional female will travel a long distance on man, but in general it is the males that thus use him. An appreciable re-infestation took place some years ago of part of Block 2 in Shinyanga, which we had cleared of flies, when a steady stream of hundreds of labourers were crossing it to and fro into the fly bush behind for material for the new township and railway. Picketing showed that the flies carried in (*G. swynnertoni*) were almost entirely males, and the invasion in this case died out after the cessation of the movement. Similar re-invasions, associated with movements of man, have taken place lately in

Shinyanga in the "Outer Circle" (*see* map 2) and in Block 5A. The former died out following picketing, the latter had to be dealt with by rather fuller discriminative clearing. That the flies may use the paths of man for their spread and not merely man himself is possible.

(c) Carriage by cattle and on cattle-paths.

Next to the flies' own movements, native cattle are probably the greatest spreaders of tsetse, in Tanganyika at any rate. There is usually in that Territory a close juxtaposition between well-stocked areas and fly areas. On the occurrence of scarcity of grass the native owners risk their animals in the fly belt. When there is any scarcity of water they do the same. The cattle go into the fly belt and out of it day after day, carrying flies back on themselves and making well-beaten paths for the flies to follow spontaneously (*see* p. 207 above). As the tsetse advances, the people are slow to abandon their grazing and their old waters; not an occasional path but fifty or a hundred or more paths to the mile, thoroughly trodden and conspicuous, reeking with the scent of cattle, persist to lead the flies, now densifying, on into the still uninfested wooding. In the past four years the fly front in Western Kondoa (*G. morsitans*) has advanced on an average three miles a year. The cattle have certainly helped it to do so. The same was noted as probably happening elsewhere also a few years ago.

(d) Carriage by game.

Where game is in similar huge numbers in fly bush, it produces paths also and doubtless has a similar effect. It is not known that either on cattle or game more than an occasional female fly will travel far without feeding and leaving, but it may not need a long journey to help to spread the fly thus where the in and out movement is daily, constant, and regular, and performed by great numbers of animals that come into contact with the tsetses already densifying. Burtt believed that the game—particularly the numerous rhinoceros and their paths—had assisted *G. morsitans* on a section of the Hika advance. Jackson, on the other hand, regards this as a matter of opinion. "I don't believe," he writes, "that game can have any effect in helping the fly to advance across suitable country. If they spread further the thinly-scattered numbers of the tsetse . . . they would, I think, tend rather to defeat the advance. Increasing density behind is what is necessary to the advance, and the fly will go on in any case independently of animals. Cattle are in a different category perhaps."

Generally the game is not in sufficient numbers to produce, we believe, an effect comparable with that of the fly's own movements and of networks of cattle-paths, but the mere presence of food in country as yet uninvaded will doubtless assist an advance.

(e) Spread as the result of hunting.

Instances have been noted, as in 1925 in Mkalama, in which constant hunting by great numbers of natives has kept the game, which was fairly abundant, much disturbed and has produced unusual game movements in and out of the fly area, which the hunters also were daily entering and leaving. It was believed that these things were largely responsible for special extensions of the tsetse (*G. swynnertoni*, and *G. morsitans* in Nzega) which were then taking place. The factor noted under (f), below, quite likely also operated as the result of the constant disturbance of the game.

(f) Spread as the result of grass fires.

We are sometimes asked "do not your organised grass fires, driving the tsetses out, lead to the infestation of new areas beyond?" The reply is "No. The flies are merely driven back on themselves, doubtless increasing somewhat the density of the flies further back, or into country in which they cannot survive. A barrier which they cannot recross must be provided; otherwise they drift back and reoccupy the country from which they were driven."

At the same time it is perfectly true that the flies move before a fierce fire; that such fires, used without knowledge or discretion, might well produce extension of fly belts; and that the ordinary native grass fire, even where not very extensive, probably aids dispersal of tsetse fly and of much else. The huge numbers of grasshoppers and other insects which leap or fly progressively in front of a grass fire must often arrive finally many miles from where they started. Many of the insects thus transplanted may end up in places in which they cannot survive; on the other hand, on the long line on which the fire concludes, suitable niches may be found and new colonies may be founded. This should apply to the tsetse flies.

(g) Automatic and unaided spread.

It is misleading to speak, as some have, of a migration of tsetse. Migration suggests a flight by large numbers of individuals across an intervening stretch, that remains uninfested, to a distant site. Tsetse flies do not thus migrate, as do birds and locusts and butterflies. They spread—or retreat. If they come to unsuitable country, and it is wide enough, it stops them permanently. If it is narrow enough they may cross through it, not over it. There is a constant small movement throughout a tsetse belt, and this with a fly population in excess of suitable density will extend its margins where suitable country adjoins. The tendency of the flies to stay together, at any rate when well fed, will tend to counteract such dispersal, as by a magnet, where the population is small. Where it is great, the flies that have wandered out will meet so many others that have done the same that it is probable that the back-pull will cease. If Jackson's observation, that the flies tend in spreading to follow the drainage valleys first, is more fully proved, it will be seen that it is easier for flies in moderate numbers to extend the areas of infestation than if they had to invade all country equally.

(h) Seasonal expansion as a promoter of dispersal.

In an area in which the flies are subject to seasonal contraction and expansion there must be an annual loss and recapture of positions. In a season which is specially favourable physically or biotically it is likely that the advance will be greater and that quite new positions, permanently tenable, may be captured from time to time from which further advance may be possible. Temporarily favourable conditions will have brought about the effect which, it has been suggested above, an extensive grass fire might produce.

It is of interest, as pointing to spontaneous movement of the flies as the main cause of spread, that the westward fly advance in Kondoa did not follow the motor road. Although well established already on the eastern sections of the road, it swung a great arm round north of it and crossed it again many miles further on. There was no game movement that could account for it, and this part of the advance was particularly rapid.

Naturally, flies spreading thus and failing to find food are likely to die.

When outside their previous borders they find game concentrations and conditions that are permanently suitable, the extension of the belt is likely to be consolidated. It is in this way chiefly that the presence of game will assist an advance of the fly.

(1) Spread as the result of hunger.

Hunger, setting all the flies travelling for food far and wide, is probably an important stimulus to really large-scale dispersal. Nash, on first joining the Tsetse Research Department, carried out an experiment on *G. morsitans* which showed that young flies travel further than old flies. Young flies that do not soon find a food animal are the hungriest of all tsetse flies. Since then Jackson has proved abundantly by means of flies marked to show place, date, and state of hunger on capture, that hungry flies travel far more freely and widely than flies that find food. The species were *G. morsitans* and *G. swynnertoni*. It is believed that too great a scarcity of food animals, or perhaps their harrying to a point which makes their habits irregular, will contribute strongly to the production of spread of the flies, though if the country into which this takes place is unsuitable in itself or devoid of food the advance will not endure.

C.—OPEN COUNTRY AS A FLY BARRIER.

1.—WHAT WIDTH OF OPEN COUNTRY WILL *G. SWYNNERTONI* CROSS?

(a) Spontaneous movement.

In June–July 1932 three miles of the clearing, 800 yards in width, that runs along the Mantine Road (*see* map 2) between Blocks 5A and 11 in Shinyanga were fenced off. Its north-west side was already bounded by a live fence of *Commiphora*. All gaps in this were stopped with posts and sticks let into the ground so that not a dikdik might pass. Along the opposite side of the clearing was placed Napier–Bax's experiment in different types of game fences, " brush " and other, thus killing two birds with one stone. Across, at the ends of the strip, ran two fences of wire to avoid the bulk and shade by means of which other types of fence might have guided the flies across. Beyond both ends of the fenced-off land the clearing ran sufficiently far, it was believed, to avoid easy outflanking by the flies. No movement across by man was allowed and game was excluded. This clearing is shown on pl. 18, fig. 1.

In all, 467 flies were captured, marked and released in the bush in the margin of Block 11. Of these marked flies, no less than eleven, or 2·4 per cent., were recaptured by fly boys working the margin of Block 5 A. In this and later experiments the hunger stage of each fly was recorded on its thorax, and H. M. Lloyd found that throughout the experiments the hungrier flies tended to cross the clearing quicker than the more replete flies, showing that they were crossing in search of food. Confirming this was the fact that the female percentage of the flies that crossed was higher than that in the total of flies that were marked.

Lloyd concluded (i) that an 800 yards clearing from which game is excluded is an insufficient barrier against *G. swynnertoni*; (ii) that the effectiveness of the clearing is the same whether the baobabs are cut down or are left standing;* (iii) that if the clearing passes through eluvial and old hard-pan patches, the flies will cross through both; and (iv) that the reason for crossing is the urge for food. For this reason roads following a clearing should be on the infested side of

* Actually when down they were still conspicuous.—C.F.M.S.

the clearing, so that flies can get a chance of feeding on traffic along the road and thus not want to go further.

This clearing was varyingly flat and concave. The bush on the Block 5A side could clearly be seen from Block 11. R. H. T. P. Harris, who conducted an experiment in Zululand in which *G. pallidipes* regularly crossed a clearing 500 yards in radius to a patch of bush in the middle, had suggested that where bush is visible across a clearing, but not otherwise, flies will cross to it (1930*a* : 71).

Moggridge, in view of his experiments to be described below, points out a shortcoming in the convex clearing. It is that objects moving in it will be visible at a much greater distance to the flies in the edge of the bush, and that they will thus fly further into the clearing to attack. This, however, will not take them across the clearing as the bush-line on the other side of a concave clearing possibly will.

In October after the grass fires had destroyed the fence excluding game from the concave 800-yard clearing, Potts found that approximately one in thirty flies succeeded in crossing it. Thus in this instance, at least, game did not appear to be assisting the flies to cross the clearing in greater numbers. One fly in 233 was found by Potts to cross a 1,200-yard clearing in October. In November, Potts failed to recapture a single fly across a 1,400-yard clearing, out of 310 marked on the other side, although 12 marked flies were caught (1 in every 26 marked) in the bush in which marking had taken place.

The time of year and the relative density of the flies are both important factors and the latter was unrecorded, so that we still do not know the full width of clearing that will be crossed without aid from man, cattle, vehicles, or game. My own belief is that any clearing less than two miles in width will ultimately be crossed by the flies without aid when they are in numbers against it.

(b) The width of clearing which *G. swynnertoni* will cross with the aid of game, and of man, respectively.

Moggridge carried out a well-planned series of experiments in the wet season from January to May, and in the dry season from August to September 1934, to test the numbers in which, the distance to which, and the conditions under which, *G. swynnertoni* would accompany (i) cattle, representing game, (ii) man, and (iii) cattle and man combined, across a clearing 1,575 yards wide. The site of the experiments was the mbuga, part naturally clear, part cleared, between the bush "island" of Sayu (*see* map 2 and pl. 12, fig. 1) and the fly bush to the south of it. In the wet season the grass was only 15 inches in height owing to a shortage of rain. In the dry season considerable areas had been burned.

In the dry season the experiments were modified to throw light on the maximum time that flies would remain on cattle, on man, and on man and cattle combined, in this wide open space. Frequent readings were taken with a whirl psychrometer and a Biram air meter to keep in touch with the weather conditions. The numbers and individuals of both cattle and man and the colours of each were kept as constant as possible.

In the first series of experiments, the making of a path resembling a much trampled game-path enabled the cattle to be trained to cross the mbuga alone. This daily crossing very closely resembled an observed crossing of the same mbuga by a herd of elands. The flies were counted on the cattle as they left the bush and the party, keeping itself carefully deflied, crossed, never less than

200 yards from the cattle, and met them at the end of the crossing for a count of the flies that arrived.

(i) *Cattle alone.*

In the wet season, in 20 crossings, (i) the average number of flies per journey that were carried across by the cattle was seven; the average time taken in crossing was 33 minutes.

(ii) These numbers, of flies carried across, were small in proportion to the numbers of flies that started out on the cattle.

(iii) The great majority of the flies left the cattle in a gorged state after travelling a short distance only.

In the dry season there were seven experiments. In these, five flies on the average accompanied three oxen for an average maximum period of 30 minutes. The longest period for which a fly was carried in the open was 1 hour 27 minutes. On this occasion the conditions prevailing resembled wet-season conditions. The remaining six experiments were in bright conditions in a moderate to high wind. The period at the end of which the last fly had departed varied from 14 to 30 minutes.

(ii) *Man alone.*

Four men carried on the average, in the wet season, eight flies over the same course as was used in the cattle experiments, at a slow walking pace which covered the course in 30 minutes.

In the severe dry-season experiments, the number of flies that set out from the bush was small—on an average, six. Four men walking in the open transported flies for an average time of 63 minutes, till the last fly left. The maximum time during which a fly remained was 120 minutes.

The flies were not disturbed unless they caused very definite pain, yet the rapid fall in the number of flies that left the bush with cattle was not repeated with man. In a number of cases no noticeable reduction in fly number was seen for quite a long period.

It is interesting to note at this point that on two other occasions parties of men were encountered and deflied in the open mbuga three miles away from the fly bush. The first party, consisting of 120 men, was, at 9.15 a.m. in cold dull weather, carrying 36 flies, of which 8 were females and 28 males. The second party, of 57 men, in warm, sunny weather, was carrying 22 flies, 8 being females and 14 males.

(iii) *Man and cattle combined.*

Here, in four wet-season experiments, a small number of flies were carried across the course described. The number of flies carried by man as against those carried by the cattle was in the proportion of 12 to 1. In the majority of cases the number of flies accompanying the party more than a few yards from the bush was small.

In the dry season only two experiments figured in this division. In these it was noticed that at the edge of the bush very many flies were on the cattle and only very few on man. The numbers of flies following from the bush diminished rapidly, as had happened in the rains, the majority having obtained their feed (from the cattle) and dropped off, but one or two individuals were carried for considerable periods—40 minutes and 47 minutes respectively. In the first of these experiments only two flies, both on man, remained after 17 minutes and the second experiment also was continued after the outset solely through the persistence of one fly.

(iv) *Conclusions.*

The cattle attracted far more flies than did man, but the very great majority of them fed immediately and left. Man attracted fewer flies, but a greater proportion of those that came followed more or less persistently. When cattle and man were used together the " feeding " flies fed quickly on the cattle and left, the flies that were out to follow followed mainly on man. Man, although attracting fewer flies at the outset, is probably specially dangerous as a carrier of tsetses across open spaces, especially as the observations showed that a considerable proportion of female tsetses might be carried. For " cattle " the word " game " might certainly be substituted at any rate as regards many species.

2.—THE WIDTH OF CLEARING WHICH WILL SAFEGUARD A ROAD FROM *G. SWYNNERTONI.*

The experiments were designed to test how far the tsetses would fly into a clearing from the fly bush, in this case to a target of three cattle and of four to five men.

Three sets of experiments were carried out, but the data obtained from the first were abandoned, owing to the discovery of a complicating factor—fly lurking in scanty felled scrub in the open. The second set was carried out under tall grass conditions, the third under conditions of almost uninterrupted vision. Both sets were carried out in the open ground between Sayu and the main fly bush (*see* map 2). In the second series (in July) the grass was, on the average, 1 foot 9 inches high (blades) and 3 feet 6 inches (heads). At 200 yards the uppersides and the backs of the oxen were visible through the grass, at 300 yards their backs, at 400 yards the upper line of their backs, but man from the waist upwards. From a height of 3 feet at the edge of the bush no movement of cattle or man could be seen at 200 yards. In the third series (in September) the grass had been burned but not cleanly : strips and tufts of partly burned grass remained. Visibility was uninterrupted (except momentarily by the unburned tufts) from a height of 3 feet from the ground.

In the second series of eleven experiments, four transects, at 100, 200, 300, and 400 yards from the bush, were slowly followed in turn. In the third, three transects only, up to 300 yards.

In the second series, with visibility restricted, no flies were captured at a greater distance from the bush than 100 yards. The total captured was 61, of which there were males 37, females 24, off oxen 59, off man 1, off the ground 1.

In the third series of five experiments the total captured was 17, of which one was captured at 300 yards, 4 at 200 yards, 12 at 100 yards.

The following conclusion may be drawn from these experiments : " For all intents and purposes flies do not attack a moving target at a distance from the bush edge of more than 200 yards." (Moggridge, who also stated, however, that he is of opinion " that results of a different nature might be expected under altered conditions of speed of movement, size of target, etc.")

A further series of similar experiments, which must here be summarised briefly, was carried out in a relatively dirty clearing. Here the contour of the ground came into play in a very interesting manner, a number of flies being taken even on the 300- and 400-yard transects where rising ground made these readily visible from the bush edge, and, it was thought, for that reason; while dead, blanketed ground on the 200 yards transect produced fewer flies than were caught at 300 yards. Though there was a greater density of the

flies on the edge of the bush in the wet-season division of these experiments, a greater range of flight from the bush-edge was noted in the dry season. This was thought by Moggridge to be due to the greater visibility in the dry season and the fact that the severe conditions then existent might militate against the occupation of the edge of the bush by any but the most hungry flies.

From the combined experiments Moggridge concluded that objects moving over level open ground will not tend to be attacked by tsetses lurking in the bush at more than 200 yards; but that if the range of vision of the flies is increased by the contour of the ground the range of attack will increase, as it did in these experiments, up to no less than 400 yards. We have considered in the past in Shinyanga that 400 yards of clearing on either side of a road safeguarded it for practical purposes from the flies in the edge of the bush. Evidently 500 yards or more would be better where objects on the road can be seen from the bush, while 300 yards might suffice where they cannot.

3.—THE EFFECT OF CONSPICUOUS STATIONARY OBJECTS IN ATTRACTING THE FLIES INTO A CLEARING.

In 1922 I carried out an experiment near Zagayu in Maswa in which I stationed pairs of catchers and bait-cattle at intervals along a road on each side of which a space of 70 yards had, on the average, been cleared. Some of the catchers without cattle were stationed at two acacia trees which had been left beside the road and at a high conspicuous white mosquito-net, erected by the road, all three objects at a considerable distance from each other. The net and the two trees attracted flies all day, 77 being taken at one of the trees which was 80 yards from the nearest bush. Elsewhere, the fly boys and cattle being largely screened by the grass, only half a dozen flies were taken in all (Swynnerton, 1923 : 334).

It has been usual to leave baobabs standing in clearings owing to the difficulty of felling them. Potts experimented with the baobabs of the Mantine Road clearing, 800 yards wide. All the baobabs were felled and the limbs cut off, as it was thought that they might be leading the fly across. Even when felled, these baobab trunks, with the sun shining on them, made a fair target. To fell and cut up a baobab cost Shs. 5/40 for labour alone, and the total cost of this work was 151/60. This made no difference to the numbers of fly crossing the clearing.

Other observations, however, suggested that the baobabs were of some importance. Three experiments were carried out by Potts in the crossing of the Beda Clearing (1,200 yards wide) by the flies (still *G. swynnertoni*). Two were carried out before the removal of the baobabs, and one after, with the following results :—

Expt. 1. October, 1932. Of 466 flies marked, 2 crossed, or 1 in 233.
Expt. 2. April 1933. Of 1,087 flies marked, 10 crossed, or 1 in 109.
Expt. 3. July 1933, the baobabs having been felled in June. Of 952 flies marked, none were captured across the clearing.

Provided that there was equal natural movement of the fly during each of the experiments, it would appear that felling of the baobabs had reduced the numbers of flies crossing the clearing.

On various occasions before the felling of the baobabs, 97 flies were taken in the course of 19 stops at these trees, *i.e.* 5·1 per tree; as compared with this 3 flies only were taken in the course of extensive wanderings in the clearing away from the baobabs. These wanderings would cover approximately

5,000 yards of clearing, as compared with probably about 1,500 yards entailed in the baobab catches. Observations since the felling of the baobabs have been meagre, but suggest a reduction in numbers of flies at them; 8 flies were caught at 4 felled baobabs, *i.e.* 2 per tree, as compared with 1 fly in the course of some 2,000 yards of wandering in the clearing.

4.—THE EFFECT OF SETTLEMENT AND THE PASSAGE OF NATIVES ACROSS BARRIER CLEARINGS.

An infestation by *G. swynnertoni* of the motor road and cattle track running along the centre of the Beda cattle-corridor clearing caused anxiety, in view of the approach of the date on which it was hoped to inaugurate the passage of cattle. This infestation was a puzzle through the fact that the clearing was 1,200 yards broad and in view of the cleanness of its execution. First, the baobabs were suspected; the investigation on them already described was carried out and the baobabs were cut down.

As the infestation still continued, Vicars-Harris (then Acting Director) suggested traffic as the cause. Fly pickets were accordingly posted by Potts to defly all traffic entering the road on paths from the fly bush. "The figures from these fly pickets are illuminating; in less than a month 1,657 flies were caught at them—*i.e.* were prevented from infesting the clearing" (Potts).

Similarly as regards the "Outer Circle" (map 2 and fig. 17). In this the fly numbers had been brought very low by discriminative clearing and grass burning in 1933, but they were rising again quite dangerously. A picket was placed in the clearing dividing the Outer Circle from Block 11, from which the infestation was suspected to come, on a path much used by natives. Following the establishment of this picket the infestation in the Outer Circle almost died out. The following extracts from Potts's report summarise the results of the various pickets employed by him from April to August, 1934.

(1) During the period April to July, the Beda Road picket prevented 3,391 flies, carried on man, from infesting the Beda Clearing and (during the first three of these months) 1,147 flies from entering the Huruhuru mbugas.

(2) The flies caught at Beda no. 1 picket varied between 1½ and 2½ per man passing, those at Beda no. 2 (Korozi's, *see* map 2) between 2 and 2½, and those at Beda no. 2 (original) between 1 and 1½, so that the monthly variations in total flies caught at these pickets is due rather to variations in the volume of traffic than to variations in numbers of flies available for carriage. On the other hand, the Mwamala figures did show a very appreciable increase during June, apart from traffic.

(3) During the period in question, 2,118 flies were prevented from entering the settlement area enclosed by the "Inner Circle."

(4) During June, July and August, 2,277 flies were prevented from entering the "Outer Circle" bush.

These results confirmed with scientific detail many previous observations of reinfestations of a clearing, or of a reclaimed area beyond a clearing, by the entry of natives on paths from the bush. Where settlement enters a clearing the effect can be most marked.

The picket on a clearing made in 1924 between Kizumbi and Samuye (map 2) took very few flies indeed until the clearing began to be settled and the settlers to enter the bush, for their needs for building, fires, medicines, etc. It was also believed that their high crops attracted the flies out. At any rate the fly takings rose considerably. I believe that no settled barriers,

unless of some miles' width, can permanently exclude the passage of *G. swynnertoni*. The flies are carried into the settlements and on to the roads by the natives using the bush—which all natives do. Many ultimately are carried right across. A barrier kept clean but without settlement is likely to be more effective despite a moderate number of game animals, for, as will have been seen from Moggridge's experiments, the flies tend to feed quickly on preferred animals, of which the ox, doubtless, is one, and to leave them. Also game when undisturbed seldom crosses directly, but wanders, grazing. It will attract flies out when in view but will hardly enable them, in this particular way, to cross, say, a two-mile clearing.

In the case of *G. morsitans* the effect of intensive human activity comes into the picture as well, and on this p. 325 below should be consulted.

5.—CONCLUSIONS.

Pending continued work on the subject the following rules may be laid down :—

As regards road clearings :—

(i) a clearing intended merely to protect a road and not to act as a barrier should be 800 yards broad at least, and, better, 1,000 yards, with the road generally running down its centre;

(ii) the clearing should be conducted on knowledgeable lines and carefully supervised, with a view (*a*) to a due increase in its width where the bush is more visible through concavity of the ground in between, and (*b*) to a minimum of re-growth subsequently, and should be clear of all trees;

(iii) if it is wished really to keep it clear of fly, no settlement should be placed in it in *G. swynnertoni* country, and all necessary paths leading into it should be picketed;*

(iv) if merely relative protection will suffice, settlement may be admitted, but infestation will be present if the fly is dense up to the clearing.

As regards broader cleared barriers against tsetse :—

(i) in the case of *G. morsitans* settlement in moderate intensity is likely to be useful;

(ii) in that of *G. swynnertoni* the reverse seems the case. If settlement be present, a width of clearing of several miles will, without extra precaution, be necessary for real safety if the fly is dense up to the edge of the clearing;

(iii) extra precaution would take the form of the employment of pickets and seeing that they did their work; a two-mile clearing first might in that case suffice;

(iv) the clearing (again for *G. swynnertoni*) must be clean if yet heavier infestation is not to beset it.

I should like to take this opportunity to deprecate the repetition of the clearings to be seen here and there in which unthorough methods were used at the outset, in which trees are left standing and regeneration is rife, and in which the natives must live in nearly as close contact with tsetse as they would in the untouched bush.

A possible means for reducing the numbers of tsetse in contact with the margin of a clearing is a very important question. Human activity itself may suffice for *G. morsitans*, but will not prevent the carrying in on man of a certain number of flies. Organised grass burning was used for the purpose against *G. swynnertoni* and *G. pallidipes* in Shinyanga, and very effectively. Not burning

* This last applies to *G. morsitans* too.

at all in a strip bordering the clearing is being used by us now in the case of the Beda corridor. Destruction of the woody vegetation in concentration-sites and their margins for a short distance back is suggested by our work in Block 5B to be useful.

With the tsetse clean gone from the neighbourhood, as has happened as the result of our measures in the case of several clearings in Shinyanga, the bush may be allowed to regenerate.

D.—DENSE THICKET AS A FLY BARRIER.

1.—THE GREAT NATURAL THICKET-BARRIER IN THE CENTRAL PROVINCE.

The thicket-barrier here referred to is the truly spectacular one which may be seen from the trains of the Central Railway almost throughout the 50 miles from Manyoni (through Itigi) to Chaya, and which, with its branches and islands, we have seen from the air to cover not less than 2,400 square miles, though it is obviously far smaller than formerly. It has been the subject of study by Burtt, whose observations and experiments are here summarised. Except for its outlying islands, it is shown in maps 1 and 6. Parts of it are shown also in pl. 17 and pl. 20, fig. 2.

(a) The geology of the thicket.*

This " Itigi," or *Burttia–Baphia*, type of thicket is confined to a light yellow clay cement or duricrust that, before the Rift movements, covered the old granite peneplain over the greater part of Manyoni, Singida and West Kondoa. The deep indentations in the thicket and the gaps that have split much of it off as islands are specially interesting, as they have been caused by erosion arising from the tilting of the country by the movements that made the great Rift. Gillman (in manuscript) has pointed out with complete accuracy that this type of thicket intrudes little on the granite of the miombo bush and the miombo as little on the duricrust of the thicket. Each needs, and obtains, different edaphic requirements. Thicket does grow in miombo (*see* pl. 6, figs. 1, 3 and 5), but it is not " Itigi " thicket except under conditions of contact and where traces of the duricrust are left. Therefore, wherever the erosion has eaten through the duricrust to the granite below, the thicket has disappeared and miombo (*Isoberlinia–Brachystegia* †) has replaced it, spreading in from outside. The gaps thus caused in the thicket grew wider as erosion extended, particularly where the country was hillier, and the thicket became split into islands. The miombo spread further as more granite was exposed, and miombo is ideal for *G. morsitans*.

(b) The character of the thicket.

The thicket itself is very distinctive, being characterised by an absence of lianas and the presence, particularly, of the following :—*Burttia prunoides* (a very handsome plant of a new genus), *Bussea massiaensis*, *Pseudoprosopis Fischeri*, *Combretum Trothae*, *Grewia Burttii*, *Baphia massaiensis*, *Baphia Burttii*, and *Craibea Burttii*. Most of the shrubs stood out from a broad base as many-stemmed bushes, but the *Craibea*, which alone is evergreen, grows erect as a small

* With acknowledgments to Sir E. O. Teale and Mr. C. Gillman.

† *See* pl. 11, fig. 2.

tree and is gregarious. Though mixed as to species and comprising within itself two distinct plant associations, one of these (characterised more strongly by Rubiaceae) being denser but lower than the other and occupying mainly the crests, this thicket presents on the whole a level-topped, homogeneous appearance, as may be seen from the photographs in pl. 17, figs. 1 and 2. Dense shade is present throughout from December to June when the thicket is in full leaf. During the late dry season the fine-twigged thicket, now leafless, of the height of a tall hazel copse, is a homogeneous pearl-brown; much sun shines through to the red-brown, beech-like leaf-carpet and, through the exclusion of wind, the heat inside the thicket is, to man, very great. By insects, however, shade is everywhere obtainable on the sides of stems and in crevices and at the bases of the shrubs. Actually, though close in canopy when in leaf, this thicket is at all times particularly open below, as may be seen on squatting and visualising the view that would be obtained by a tsetse fly.

(c) The fauna of the thicket.

Elephants have many well-defined roads through the great thickets, which they traverse seasonally in considerable numbers during migration. During the dry season they break their way through the thicket generally in their quest for *Grewia* seeds, of which they are particularly fond. A single or sometimes a pair of rhinoceros visit the Beruda thicket about October every year and others occur elsewhere. The greater kudu lie up in the thicket during the day-time, but come out at dusk to feed, being specially fond of deserted native cultivation. Wart-hogs are very common and appear to live in burrows in the thicket. At dawn they come out to root and feed in the " transition " and " hard-pan " areas, while during the heat of the day they drink and bathe in pools in the watercourses. Bush-pigs are common in the thicket. Animals generally, such as roan, eland and the various carnivora, use the paths made by the elephants. Dikdik inhabit the thickets and their neighbourhood. Elephant shrews and smaller mammals, as well as ground-haunting birds—pittas (*Pitta angolensis*), francolins (*Francolinus hildebrandti* and *Francolinus coqui*) and crested guinea-fowls (*Guttera*)—are present in considerable numbers. There is no lack of food for the tsetse.

2.—EARLIER OBSERVATIONS ON THE EFFECT OF THICKET ON *G. MORSITANS*.

It was realised early (R. W. Jack, and later independently myself, 1921 : 345) that *G. morsitans* did not favour dense bush. This was confirmed as regards the Itigi thicket early in 1926 by Swedi, our Department's head fly boy, who of his own initiative carried out well-planned observations on the strength of which I concluded that it was probable that really dense thicket, even low and deciduous, might be used as a barrier against fly. The Itigi thicket was therefore further investigated in July 1926. (when leafless) by Potts, Burtt, and Wallace. Swedi's result was confirmed, but it was noted that a small proportion of the flies would follow a person in. Yet further apparent confirmation was forthcoming in 1927, when it was ascertained that the Itigi thicket was still acting as a barrier to the great fly advance on Singida, though two narrow gaps in the extreme north of the thicket were being passed and it was in danger of being outflanked.

3.—INVESTIGATION OF THE WIDTH OF DECIDUOUS THICKET NECESSARY TO FORM A BARRIER AGAINST *G. MORSITANS*.

(a) The original scope of the investigation.

These five questions were asked :—

(i) Do flies enter the thicket uncarried ?
(ii) Are any carried into the thicket on animals ?
(iii) How deeply do they penetrate this Itigi-type thicket by themselves or on animals ?
(iv) Do they fly over the thicket or find their way through it low down ?
(v) Are paths through thicket a danger ?

(b) The selection of the sites for the experiments.

In 1931 Burtt, assisted by H. Harrison, was set the task of planning and making a study of these thickets and ascertaining if possible by experiment the maximum width of Itigi thicket which *G. morsitans* would cross unaided. A series of well-planned and closely-recorded experiments eventuated during 1931–33.

Burtt was assisted to select the thicket strips which would form the site of his experiments by the hiring of an aeroplane from the Survey Department. In this very flat country this aid proved invaluable. The sites selected were :—

For experiments (*c*) and (*d*) below, the Ulimiri thicket, just south of the railway station of Kazikazi; a traverse here afforded by an elephant path measured 2,600 yards.

For experiments (*e*) and (*f*), the neck connecting the thicket known as Beruda with the main Itigi thicket. This thicket neck was 1,800 yards in width on the windings of an elephant path. (The map in pl. 20, fig. 2, should be consulted and also pl. 17, fig. 1.)

The earlier experiments were conducted in the months September to November, when the thickets were leafless, full of light, and most easily traversed by game and flies. Each series and the conclusions therefrom will for convenience be given separately though they cover in part the same ground.

(c) The Ulimiri thicket experiments (Kapetu path).

These occupied the periods from 29th October to 3rd December, 1931, and from May 1932 to April 1933.

(i) *Preparatory work.*

Four clearings were made in the south side of the Ulimiri thicket adjacent to thick fly occurring in *Terminalia–Combretum* interzone savanna wooding between the thicket and the mbuga. The clearings were partial only, trees and shrubs being left dotted through them to simulate the fly bush outside with a view to their being retentive of any fly that might enter them. The clearings, the long sides of which were parallel to the edge of the thicket, were :—

(α) the " 50-yard barrier " clearing, fenced against game, 50 yards wide by 300 yards long and 50 yards inside the thicket (shown unfinished in pl. 17, fig. 2);
(β) the " 100-yard barrier " clearing, 50 yards wide by 200 yards long and 100 yards in, unfenced;
(γ) the " 400-yard barrier " clearing, 50 yards wide by 200 yards long and 400 yards in, unfenced;

(δ) the "900-yard barrier" clearing, 50 yards wide by 200 yards long and 900 yards inside the thicket, unfenced.

That is to say, barriers 50, 100, 400, and 900 yards wide respectively, of natural thicket separated the clearings from the open savanna fly bush outside.

(ii) *The main experiment.*

The experiment was planned in order to find out to what extent, relatively, flies penetrated to these several clearings, which were so placed as not to mask one another, in the dry and wet seasons respectively. The observations were obtained from a daily fly round on which catches were made, and on which equal periods of considerable length were spent both inside and outside the clearings. Every precaution was taken to preclude the carriage of flies by the party into the thicket-clearings. The "50-yard" clearing was surrounded by a heavy game-fence of brush laid horizontally between uprights and tightly packed down which excluded even the smallest non-climbing animals. Flies in the savanna wooding opposite the different clearings and also inside each clearing were marked differentially with oil-paint. The fly round was in operation in regard to the 50- and 100-yard clearings from May 1932 to May 1933, and in regard to the 400- and 900-yard clearings from August 1932 to May 1933.

(iii) *Conclusions drawn from the main Ulimiri thicket experiment.*

The following conclusions emerged from the main Ulimiri thicket experiment:—

(1) Flies were found in thicket of the Kazikazi type in the leafless season, but in far smaller numbers than in the savanna wooding outside—the proportion in relation to these latter having been only 7 per cent. in the 50-yard clearing, 0·3 per cent. in the 900.

(2) The flies penetrated to depths of 400 and 900 yards in far smaller numbers than they did to a depth of 50 or 100 yards (note the above percentage).

(3) The marked-fly figures showed that there was movement of the flies between the outside savanna bush and the thicket and within the thicket itself—whether they enter independently or on animals.

(4) A striking fact was that the incidence of the flies in the outer portion of the thicket (*i.e.* in the 50- and 100-yard clearings) varied much during the experiment, yet the fly numbers in the inner portion (400- and 900-yard clearings) did not. This is shown in fig. 21.

(5) The variation in the outer portion of the thicket was not correlated with variations in the numbers of flies present on the thicket margin outside, but did appear to be correlated with the state of the thicket itself. When the thicket was in full leaf, flies were practically absent, but increased as the thicket became leafless and decreased again as the thicket regained its leaves.

(6) The hunger figures were not capable of the simple alternative explanation, that it is the hungry flies of the population outside which penetrate the thicket, or that the flies that have entered it fail to find food and get hungry. It would appear rather that during the time when the thicket is least popular, when it is leafy, it is only the hungriest flies of the community outside, and not many of them, that enter it, but that as it becomes more leafless, thereby approximating to the state of the country outside, the flies become more hungry generally and the hunger of the flies found in the thicket is virtually the same as that of those outside.

(7) A clearing 100 yards wide was finally made outside the 50-yard thicket

barrier to produce the combination of a narrow thicket-barrier and a narrow cleared barrier. It did not lessen the numbers of flies that penetrated to the clearing in the thicket—most of them doubtless being wanderers in the thicket already. The numbers fell, it is true, but the number of flies entering the experimental clearing a hundred yards in (with no clearing outside) showed a corresponding drop during December, due undoubtedly to the re-flushing of the thicket. It was shown not to be due to a lessening of the hunger of the fly.

(8) Prevention of game-movement through the 50-yard thicket barrier by means of a fence apparently did no more than compensate for the narrower width of the barrier, for the number of flies caught inside the unfenced 100-yard barrier was virtually the same. Between 10th May, 1932, when the 50-yard clearing was finished, and 15th July, when it was fenced, wart-hogs, dikdiks, and an occasional leopard wandered into this clearing and a total of 39 flies (less than 20 a month) were taken. During the dry months succeeding more and more flies were taken in it to a total of 581—or roughly 116 per month—between 15th July and 21st December, despite the presence of the fence.

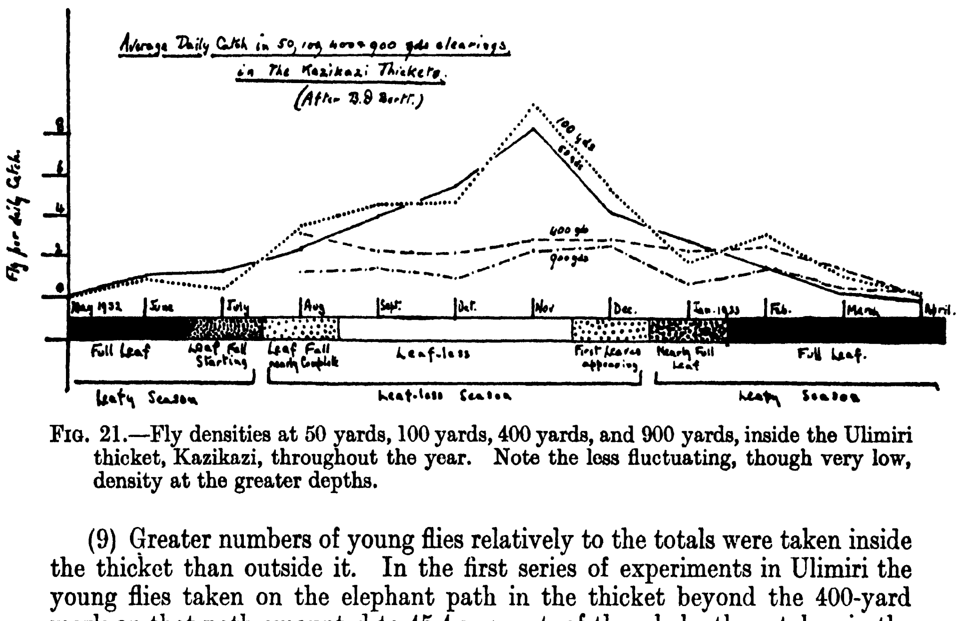


FIG. 21.—Fly densities at 50 yards, 100 yards, 400 yards, and 900 yards, inside the Ulimiri thicket, Kazikazi, throughout the year. Note the less fluctuating, though very low, density at the greater depths.

(9) Greater numbers of young flies relatively to the totals were taken inside the thicket than outside it. In the first series of experiments in Ulimiri the young flies taken on the elephant path in the thicket beyond the 400-yard mark on that path amounted to 45·4 per cent. of the whole, those taken in the first 400 yards of thicket to 21·8 per cent. and those outside the thicket only to 11·8 per cent.

(10) Examination of the marked-fly recaptures showed that the precautions taken to prevent the carrying of flies from one section to another were effective.

(iv) *Experiment to test whether the flies went into the thicket independently.*

An experiment was made to test whether the flies went into the thicket independently. During the whole of 9 days—5 days in August and 4 in November (flies very abundant outside)—catching went on continuously from 8 a.m. to 4 p.m. in the cleared plot 50 yards back. Marking of flies had been going on outside for several months previously. During the 9 days, 14 marked flies were caught in the clearing. Of one of these, caught with the paint still very wet, it can be said that it must have entered the thicket spontaneously, as

owing to the presence of man both in the clearing and 50 yards away outside, but not passing between, it was certain that no large animals could have entered.

(d) Special experiments in Ulimiri to test whether the flies pass over thicket or through it.

(i) *The first experiment.*

Burtt selected two trees at the south end of the Kapetu path, which was also the end at which the savanna just outside was best infested. One of these trees (no. 1) stood about 70 yards inside the thicket, and was conspicuous, topping the general thicket, and off the path. The other, a similar tree, no. 2, was 30 yards outside the thicket, 100 yards from tree no. 1, and stood in dense fly—off the path. About 15 feet up in each tree and overlooking the thicket a machan or platform was made—flimsily, to avoid hiding its occupant. The latter was highly conspicuous also through his constant movements in driving away the sweat-bees.

For one hour each day during seventeen days each machan was occupied, Burtt taking his turn at one or other of them daily and an alert fly boy occupying the other tree. During this hour the remaining fly boys executed a marking of tsetse round tree no. 2 (outside the thicket). They would walk away from it for 100 yards at a time in different directions and get covered with flies. These they would catch, mark, and release. They marked in all in the 17 hours 901 flies, yet the occupant of no. 1 tree, in the thicket, during the whole of the period, neither saw nor heard a single fly, while the occupant of tree no. 2 saw plenty of flies at the catchers below and even directed their catching, but saw and heard none higher up, and only one fly came to him. This had just been marked and, flying straight up, as captured flies often do on release, settled on him. Moreover, it was noted each time that the climber ascended this tree that the flies which were on him left him as he climbed up.

Both this striking experiment and the small number of marked flies retaken on the other side of the thicket in the special experiments across the Beruda thicket-neck (5 flies and 17), and across Ulimiri (3), suggested strongly that *G. morsitans* does not readily fly over thickets.

A possible flaw in the machan experiment—the fact that the flies leaving the climber or not going to him had a counter-attraction in the people below—may be cancelled out by a previous series of daily observations extending over a month, in which Burtt, watching elephants visiting a fly-concentration site from a machan at Sambala, noted that the flies (*G. morsitans*) each time left him as he ascended. Only twice was he bitten in the tree, probably by a fly carried up. There was no one below.

(ii) *The second experiment.*

On 22nd, 23rd, and 24th November, 1932, five observers, with conspicuous success of the type shown in pl. 10, fig. 3, were placed inside the thicket on machans in trees from which they could overlook the general leafless thicket top and at distances varying from 10 to 70 yards in from the thicket margin at approximately 14 feet from the ground.

No flies were seen at four of the screens. During the first two days three flies were captured on the fifth screen, about 50 yards inside the thicket; but it was found that the catcher at the screen was sitting below the screen at about 10 feet from the ground, while a second screen had been placed at 7 or 8 feet from

the ground by mistake. The lower catcher was on the ground and the whole formed a ladder for the flies to ascend. The third day, when this error was corrected, showed no flies.

Simultaneously on the same dates five observers were stationed similarly beside blanket screens near ground-level from 10 to 70 yards from the thicket margin. These observers captured flies sporadically through the day. Further and confirmatory experiments were carried out on 30th November, 1st December, and 22nd and 23rd December.

These experiments suggested that the flies pass underneath the thicket canopy and not over it.

(e) The first Beruda thicket-neck experiment (27th September to 15th October), and the width to which *G. morsitans* will penetrate Itigi-type thicket.

Flies were abundant on both sides of the neck; 1,931 flies were marked with oil-paint during the seventeen days of the experiment on either side of the thicket-neck, outside it. Of these, only six were met with again on the opposite side of the neck, though very numerous painted flies were seen on the side on which they were marked. Burtt and his fly boys traversed the path daily, but he was convinced that his precautions were sufficient to avoid flies being carried through by his party. A careful watch was kept for spoor. A giraffe had passed through the day before the experiment and on its last day a black rhinoceros did so. Between these dates only hyaenas and members of the cat family passed on the path, the latter including a lion and a leopard. Their passage could have accounted for the six flies caught that went through, but it will be seen that the likelihood that the flies passed through otherwise is greater.

(f) The second Beruda thicket-neck experiment (October 1933).

In this, to avoid any possible carrying through of flies, Burtt and Harrison each took a side of the neck. Food was conveyed to the further party once a week by a roundabout route of 22½ miles from Kazikazi, itself some miles from the neck, and, to make assurance doubly sure, the lorry that took it was systematically searched and showed no coloured flies. Of 2,012 flies marked 17 were taken on the opposite side of the thicket-neck.

The questions then to be answered were "Had the flies followed the path through or, wandering about in the thicket, had they merely accidentally emerged on the opposite side?" These questions were answered by experiment.

(g) An experiment in the Beruda and the Ulimiri thicket jointly.

Screens watched by fly boys were set up on the Kapetu path in Ulimiri and on the motor track to the "Racquet" in the Beruda thicket (*see* pl. 20, fig. 2) at 25, 50, and 75 yards along the paths and the road respectively. Only 4 flies were taken in 80 hours' observation on the road (10 a.m.–2 p.m. daily from 24th July to 9th August, 1933), all at the 25-yard point. In Ulimiri 9 flies were captured at the 25-yard point on the path, 5 at the 50-yard, 1 at the 75. Outside the Ulimiri thicket at the exit of the path the flies were very dense —100 per boy-hour. The same was true of the flies in the savanna at the end of the motor track. The contrast between 15 flies in 144 hours on the path and 100 per hour outside (*i.e.* 1 : 1000) suggested that the flies were not using the path in particular as a usual means for entering or traversing the thicket.

A further experiment at the Beruda thicket-neck was carried out in amplification of the above experiment. The two European observers took up their

station at 800 and 900 yards along the elephant path with screens. At 50–60 yards on either side of each in the pathless thicket a fly boy was stationed with a screen. Observations took place from 9 a.m. to 12 a.m. for five days from 20th November, November being the month in which the flies most entered the thicket. The usual extreme care in deflying was taken. In all, seven flies were taken in the thicket, only one on the path.

(h) Conclusions drawn from the above experiments.

An extremely small proportion of the flies present outside are continuously entering the thicket, spontaneously or on animals in the leafless season, and wandering in it. A very few eventually get through thicket a mile in width.

Having given the conclusions for each set of experiments we may consider their bearing on the questions originally asked.

(i) *Did the flies enter the thicket uncarried?*

It was strongly believed that the flies enter the thicket uncarried, but the case of the fly with wet paint referred to above was the only quite unchallengeable piece of evidence.

(ii) *Did the flies utilise animal transport?*

Certainly, on man, they entered in large numbers both on the path and into pathless thicket when leafless. In addition, flies were found at a wart-hog shot 300 yards inside the thicket on the path, as flies had also been found at a bush-pig shot 400 yards inside similar thicket at Matelele in 1928 by Burtt. Harrison, who has done much elephant shooting in this Itigi country, believes on indirect evidence that flies are carried into the thicket by elephants in considerable numbers. Animals are probably thus quite largely responsible for the flies that were found wandering in the thicket, but it is notable that the flies were not found there when the thicket was in leaf.

(iii) *How deeply do the flies penetrate Itigi-type thicket, by themselves, on man and other animals, or on vehicles?*

Flies penetrate to at least 50 yards uncarried by animals (the fly with wet paint). They penetrate also to a mile in extremely small numbers, whether aided by animals or not is in this case still unknown, though probably the animals are not necessary. Out of 387 flies marked by Burtt on the Kapetu path in the thicket from first to last only 3 were recovered outside.

During 18 experiments by Potts, Burtt, and Wallace in July 1926 the " followings " tabulated below took place on man :—

No. of flies	Distance followed in yards
27	50
19	500
18	1000
10	2000
2	4000
1	6000

Considerable numbers of flies regularly rode on Burtt's lorry and bicycles through the 6,000 yards of thicket connecting the " racquet " with the fly savanna to the south; we have also seen flies carried through the great thicket on the trains from Kazikazi to Manyoni (50 miles).

(iv) *Do the flies pass over thicket or through it?*

Flies pass through thicket. The negative but consistent evidence of screen experiments seems to indicate this.

(v) *Are paths through thicket a special danger?*

Despite the contrary result of the second experiment under (f), above, the flies were taken on the Kapetu path (Ulimiri thicket) in far greater numbers than off it, including those portions of the path that traversed the centre of the thicket. Animals, hoofed and padded, were crossing this path in fair numbers or using parts or the whole of it, and the flies may either have been carried in on the path or been carried on to it from the thicket and, finding it, stayed on it. In the latter event, the paths were providing the flies with a hunting-ground on which animals would be more easily found. In the former alternative the path may have been important as attracting man and some species of game to enter and traverse the thicket, which otherwise they might not have done. This is in any case true of man, and it is also true that many animals traverse thicket on elephant paths which do not normally use it.

(vi) *General conclusions.*

The Itigi-type thicket when leafless admits flies in small numbers all the time. The penetration to 900 yards as compared with that to 50 is as 0·3 : 7 per cent. of the numbers in the savanna outside, so that it is probable that with greater depth a distance would be reached beyond which for practical purposes no flies would penetrate. Whether the flies would use the thicket as much as they do if game were absent, or would penetrate as deeply as they do if game were excluded, is unknown.

In Nigeria (Lloyd, Johnson and Rawson, 1927 : 427) *G. submorsitans* definitely uses more or less evergreen river-bordering thicket as a dry-season retreat under the intense desiccation obtaining there. There appeared to be indications at Kandaga, in Kondoa-Irangi, that something of the same kind, but on a much lesser scale, was occurring there.

The small numbers, however, in which the flies were present even in the leafless thicket (away from its margin and from the Kapetu path) is illustrated not merely by the percentages quoted above, but by the results of traverses. Five long traverses (from one to two miles each) were made by compass by Burtt himself through the pathless portions of the Ulimiri thicket as well as, for a time, by Burtt, a regular daily traverse. The latter, accomplished 17 times, covered a width of thicket of the rather more open type of 2,200 yards, from 400 yards inside it to its southern margin. Between this 400-yard point and 70 yards from the margin only one fly was caught, although in the open bush just outside 901 flies were caught in an hour's catch daily during the 17 days. The five long traverses yielded only three flies between them. Two of these three flies were taken at fresh elephant tracks in the densest part of the thicket. When the Itigi-type thicket was in leaf practically no flies could be caught in it.

It would have been pleasant to be able to record that a mile's width of deciduous thicket will definitely exclude all *G. morsitans*. In practice, however, in country in which exclusion of grass fires will produce strong densification at all, it is nearly as cheap to create a barrier two or three miles in width as one of 500 yards. That evergreen thicket—which in dry country may be manyara, in damper, *Cupressus* plantations—is likely to exclude this type of tsetse in very small width is suggested both by the leafy-season results at Kazikazi and

by the effect of planting at Shinyanga, which will be referred to below. It would seem that any barriers of the kind will have to be fenced against the free passage of game.

4.—EXPERIMENTS IN THE FORMATION OF THICKET IN SHINYANGA AGAINST *G. SWYNNERTONI* AND *G. PALLIDIPES*.

(a) Thicket mainly natural and deciduous.

(pl. 11, fig. 3.)

The natural thickets surviving in Shinyanga probably represent in part the original denser covering of the area before the advent of the grass fires that accompanied habitation by man; but they occur now in very small patches and narrow strips, the latter following the watercourses. They differ much from the "Itigi type" thicket. They are far denser low down and much intertangled with climbers including *Ipomoea pilosa*, *Hippocratea Loesneriana* and the four woody climbing Combretums (listed on p. 319 below), *Markhamia acuminata*, *Abrus Schimperi*, *Commiphora Stuhlmannii*, *Fagara Merkeri*, and (on hard-pan and semi-mbuga) *Ormocarpum trichocarpum*, with *Dichrostachys glomerata*, are amongst their common shrubs and trees. They promise, if continuous, to form a better fly excluder than the Itigi type.

Fire continues to be excluded from the 300-yard barrier of deciduous thicket (map 2 and pl. 12, fig. 1) referred to on p. 20 of my report for 1930 and figured therein at p. 17, and a really good and, on the whole, even thicket is resulting, which is quite striking when it is in leaf. Good stands of *Abrus Schimperi*, *Markhamia acuminata*, and *Dichrostachys glomerata* have arisen, *Grewia platyclada* and *G. bicolor* have grown up between, and the whole is being matted together by numbers of the four common climbing Combretums, as well as by other climbers. Though it is not a complete fly barrier yet and probably in its present width never will be, it is at least so effective that one now rarely sees a fly on the road that runs down its side and on which tsetses used to swarm. Tested lately, in the wet season, no tsetse could be found along it.

Part of the 1,000-yard deciduous barrier was absorbed after one year into Block 10A, when this was devoted to non-burning, and the whole will shortly be indistinguishable from it. The important result already emerging from it is that, though it has still many gaps and is lower than the 300-yard barrier, the old Mwanza road, which it was designed to protect, has for two years past carried very little fly indeed despite the fact that the latter used to be pestiferous here and that plenty of flies still exist in Block 9 alongside. Flies taken on the sections of the round of Block 10A which tap this thicket barrier amount only to 16·1 flies per 10,000 yards.

(b) Thicket mainly planted, and preferably evergreen, at Shinyanga.

(i) *General note.*

Naturally where we can get effective thicket cheaply by mere exclusion of grass fires we shall not plant it, unless with species from which profit may be made, but natural thicket cannot be obtained with speed under certain widespread conditions, and here it may be necessary to plant. It may be necessary also in any barrier to plant certain patches that will not go to natural thicket where these patches happen to cut across it.

In first planting a barrier, cheap transportability of the material to be used

is important. This gives a preference to species grown from seed over those grown from cuttings, unless the latter are obtainable in quantity locally. In the case, however, in which it is proposed to plant *Euphorbia Tirucalli* (manyara), which grows only from cuttings, in a locality in which it is non-existent, it should be possible, if time were available, to grow large initial plantings of it two years beforehand and then plant the rest of the barrier from cuttings taken from these.

Secondly, it is most necessary for the avoidance of nursery and transplanting expenses to have species that will grow freely at stake—that is, when sown as seed or planted as cuttings in the site in which they will finally grow. This advantage, as regards seeds, applies especially to Ceara rubber of the species mentioned below, and as regards cuttings, to manyara.

(ii) *Manyara thicket* (Euphorbia Tirucalli).

Our manyara (*Euphorbia Tirucalli*) thicket, described and illustrated in the annual report of the Tsetse Research Department for 1930 (p. 19), has come on fairly rapidly and on well-drained ground is already everywhere well above a

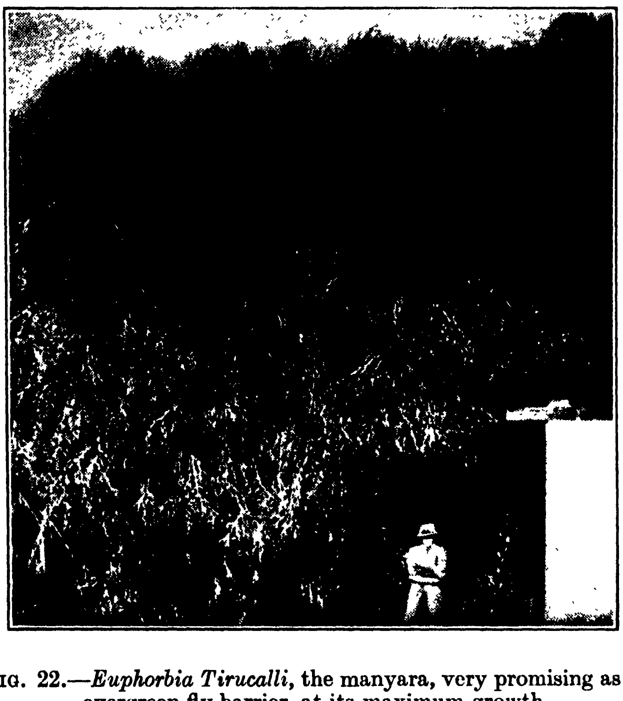


FIG. 22.—*Euphorbia Tirucalli*, the manyara, very promising as an evergreen fly barrier, at its maximum growth.

man's head, ten feet being a common height here. It has its poor parts, mostly in height-growth rather than density, and small natural thickets which were left interspersed give the impression of partial interruption when they are not in leaf. But in health, at least, it looks splendid and it has made a really dense mass of dark evergreen foliage. On all ground it grows fastest beside a small trench, as along the roadside, and to get it to do well on the hard-pan portions of the strip these had to be ridged or lightly trenched. This has been quite effective, but it is here that the height-growth is slow. Manyara suffers much

from the competition of grass before it shades the ground and needs weeding in the rains until it does shade it. This—and this only—has made the experiment expensive.

For this reason and because labour is difficult to get in the rains, it would be best in long-grass country to plant the Euphorbias in rows about 12 feet apart, to allow ox-drawn cultivators or light ploughs to weed in between until it has out-shaded the grass. Manyara is best planted in the dry season, say in August, for it tends to yellow and die at the "collar" if planted in the rains, though shading of the ground just round it tends to obviate this. It is browsed in time of drought by herbivora, especially by greater kudu and rhinoceros. It has nevertheless succeeded at Shinyanga, and all really depends on the numbers in which the animals are present relatively to the amount of manyara.

In a hollow which in the rains sometimes remains flooded back from the Ningwha river for a fortnight together, the *Euphorbia* has failed completely. However, some indigenous species of shrubs grow well there, including the excellent climbing Combretums and *Harrisonia abyssinica.* Trial plantings of several other species have been made in it and the following are, so far, succeeding:—*Melia azedarach* and *Cassia siamea*—both excellently, as also a few *Dodonaea viscosa. Bougainvillea glabra* and *Rhus viminalis* have made a moderate start. There has been an extraordinary spread of close-standing young *Acacia campylacantha* right across the hollow area from a few large trees since the fires were excluded, testifying to an unexpected range of seed dispersal in this species and an independence of stimulation by fire. A combination of *Melia azedarach* and the *Harrisonia* is proposed for the filling of the gaps in this place.

The manyara barrier, 100 yards wide and 1·74 miles long, is already becoming very effective. In a test carried out down either side of it and of the 300-yard deciduous barrier mentioned above, a total of 34 flies (or 77·2 per 10,000 yards) was taken on the infested side of the barrier and only 4 (or 9 per 10,000 yards) on the protected side. These four flies were all taken at the two remaining weak spots in the *Euphorbia.*

(iii) *Experimental plantings of various species.*

St. Clair-Thompson, before leaving Shinyanga, carried out some considerable plantings on sandy granite soil, on hard-pan soil, and on black alluvial mbuga on the Ngongho river. The object was to discover the plants that would form planted thicket most cheaply and easily. Amongst other species, eucalypts, pines, and cypresses were tested. The result was that the plantings on the granite and the hard-pan all failed, except chiefly for a row of *Rhus glaucescens* on the former, but indications came therefrom which have helped in the selection of species that have been planted since and that are succeeding. Thompson's results on the black alluvial soil have been better as regards the species to be tabulated below.

The granite area was replanted in November 1932 with small plots, each of a different species or combination of species, that it should form a model fast-growing thicket of great density and thorniness. Elephants will go through any barrier and can only be excluded by shooting, but there are species of game which fight shy of a fly barrier of the type here proposed, and if they can be excluded as well as the flies it will be something gained. The standards—trees and shrubs of erect growth—that have been used in this experiment may be deduced from the names given below. The thorny climbers planted with the standards, to entangle and densify them into a

thicket, included *Combretum trichopetalum*, *Bougainvillea glabra*, *Harrisonia abyssinica*, *Acacia pennata*, and *Caesalpinia sepiaria*. An experiment had previously been carried out in the uprooting, rootstock division, and replanting of the four trailing Combretums, everywhere abundant in the bush—*C. purpureiflorum*, *obovatum*, *longispicatum*, and *trichopetalum*. Only the last had given a satisfactory survival and was used further.

The hard-pan patches which border and intersperse St. Clair-Thompson's black alluvial mbuga referred to above, and on which everything had failed, were at the end of 1932 ridged and replanted, partly with likely exotics (Ceara rubber, *Euphorbia tirucalli*, *Cassia siamea*, etc.); partly with native species that grow naturally on hard-pan, such as *Commiphora Schimperi* and *Lannea humilis*, these being all planted as standards; and partly, to entangle and densify all these, the climbing Combretums and *Harrisonia*. These new lightly-ridged plantings are already man height or more and they give very great promise. St. Clair-Thompson's main hard-pan experiment (elsewhere) was abandoned, as survival was of the scantiest.

Successes so far both on black-alluvial mbuga and granite.	Failures on both.
Manihot glaziovii	*Carissa grandiflora* (nearly succeeds)
Euphorbia Tirucalli	*Dodonaea viscosa* (nearly succeeds)
Schinus molle	*Eucalyptus* all spp. (failed through termites)
Melia azedarach	*Cupressus arizonica*
Moringa pterygosperma	*Cupressus lusitanica*
Cassia siamea (best on granite)	*Callitris robusta*
Lycium horridum (a thorny shrub from the Karroo)	*Pinus longifolia*, *pinaster* and *halepensis*
Rhus glaucescens (slow)	*Solanum aculeastrum*

Comparative failures on the granite, more successful on the alluvial include *Rhus lancia* (chiefly on and for some distance round old decomposed termite-mounds), *Caesalpinia sepiaria* (Mauritian thorn—many deaths and much die-back in a very dry season), *Aberia caffra* (healthy on mbuga, but growing very slowly).

Failures on the granite, untried on alluvial include *Jatropha curcas*, " mbono " or " physic nut " (failed through termites), and *Hakea suaveolens*.

Successes on the granite, hardly tried on alluvial, include *Rhus viminalis* (very fast growing but " leggy "), *Leucaena glauca*, and, so far, *Fourcroya*.

Still doubtful is *Synadenium Grantii*, which, despite its villainously acrid juice, is attacked by termites—possibly after dying underground. *Dodonaea viscosa* has grown fastest and most luxuriantly of all, but half-way through each dry season large numbers begin to fail and these die before the rains can rescue them—in their second season particularly. The Mauritian thorn (*Caesalpinia sepiaria*) has behaved not dissimilarly under Shinyanga conditions. The Eucalypts planted included *crebra*, *polyanthema*, *Bridgesiana*, *rostrata*, *saligna*, *microcorys*, *siderophloia*, and *amygdalina*. All started promisingly and all were exterminated by termites. *Thuya orientalis*, the Oriental Cypress, had done well till the specially dry season of 1934, when a considerable number of the trees would have died if they had not been assisted with water. Next to *Euphorbia Tirucalli* this would have made the best evergreen barrier of the trees that appeared to be succeeding.

The original treatment on each of the soils was ploughing. Weeding has continued since, at least once a year. A great hailstorm of heavy stones on the 10th February, 1935, damaged the plantings on the granite very greatly, and the stems and branches of the trees and climbers still show great wounds and weals.

5.—EXPERIMENTS IN PLANTING THICKET IN ITUNDWE, KONDOA-IRANGI, IN MIOMBO COUNTRY AGAINST *G. MORSITANS*.

The natural conditions under which the plantings here have taken place are typical, probably, of a great deal of *morsitans* country. They are far more favourable to tree-growth than are those of Shinyanga, and they have already given clear indications as to what species are and are not likely to be worth using.

In the following brief account the differential effect of initial treatment of cover and soil is not dealt with. Actually various methods of transplanting were tried as well as spot sowings (to the number of 99,000) and pit-plantings (70,000). These numbers are for 1929–30 alone. Plantings were also made at Salanga on the top of the scarp. The work was done by St. Clair-Thompson under the initial planning and direction of Phillips. After the first season weeding was discontinued, but the plantings were protected from fire. I last inspected the Itundwe plantings on 9th June, 1934. They fall broadly into three groups, if the high-level plantings on Salanga Hill are excluded :—

(*a*) Plantings near the house, made in 1928–29, on a fairly good granite soil on the instep of the foot of the east-facing Masai scarp, originally miombo wooding but characterised now, in regenerating native fields, by much *Combretum Zeyheri*.

(*b*) Plantings in miombo wooding, the latter ring-barked or felled, fair soil for miombo granite, carrying fairly good grass and readily densifying through its own sapling growth and an upgrowth of the tall shrub *Indigofera gyrocarpa* when fires are excluded, planted in 1928–29.

(*c*) Plantings at the " bad " end * of the protected miombo strip, grass and densification power much poorer, planted in 1929–30. (This plantation, a long strip, presently leaves the miombo, crosses a narrow mbuga of black, cracking alluvial soil and embraces at its eastern end a gentle slope of good and friable soil with trees of *Acacia spirocarpa*.)

Only a portion of the results noted need be mentioned here. In the plots at the house, which are 5½ years old, the Eucalypts, which had done well previously, were in course of being destroyed by termites. *Schinus molle* was now dying at 15 feet high (in June 1934), having previously appeared to do well. *Cassia siamea* and *Morus indica* (small-fruited mulberry) were well-grown and happy. *Melia azedarach* was stag-horned, leafy below. The *Cassia didymobotrya* were all dead after having made a magnificent growth, evidently merely short-lived. The *Rhus lancia* were good, up to 15 feet high.

In the miombo plantings (*b*), which are 5½ years old, the densification was good, as stated above and as shown in pl. 11. *Eucalyptus Bridgesiana*, *polyanthema*, *robusta*, *crebra* and others, had all done more or less well, the first especially making a good and even height-growth despite the competition of the grass; but most were now, for the first time, being destroyed by termites. The *Hakea suaveolens* were mostly now felled by termites, after making a

* *See* p. 276.

very excellent, dense covert 12 feet high. *Dodonaea viscosa* had made an excellent thick covert 15 to 19 feet high, but is losing heavily, perhaps partly owing to over-close planting (3 feet), probably more through mere lack of longevity; it is said to be short-lived as a hedge-plant in Southern Rhodesia. One dead individual on the margin when dug up showed no sign of termite attack; another plot 12 to 15 feet high was also losing. This species grows naturally and reproduces well on the summit of the scarp, and, as stated, had grown splendidly here at its foot, but despite an abundant production of fruits each year, no regeneration had occurred.

Other trees were: *Acacia Baileyana*, from 12 feet (one individual) to 26 feet. Casuarinas from 10 to 20 feet high. *Cassia siamea*, one plot from 16 to 27 feet, very green, thoroughly expansive and happy. In joint plots of this and *Jatropha curcas*, the latter was 8 to 12 feet, apparently forced up by the *Cassia*. The miombo here had been felled, some was dead, and some was re-shooting. A similar plot under untouched miombo, though with canopy not unbroken, had failed, mostly dead, a few *Jatropha* surviving and fewer *Cassia*, the latter only 2 to 3 feet high. This applies also to a patch where canopy was completely absent: perhaps due to the competition of the miombo roots. In the ring-barked miombo *Cassia siamea*, sown at stake, was good, 27 to 30 feet, the best individual being 32 feet. The *Jatropha* were 6 to 11 feet. Trees under half-dense shade of *Strychnos Burtoni* were growing healthily but were spindly. *Schinus molle* was from 6 to 14 feet high, but not entirely happy. *Afzelia quanzensis* (a fine native tree and timber), spot sowing, was from 2 to 5 feet high, but formed quite a thick stand and was very healthy; there was but little overhead shade though the *Afzelia* was good even where it occurred, as under a spreading *Combretum apiculatum* or *Zeyheri*; medium good soil.

Among the shrubs, *Caesalpinia sepiaria* had made a good stand but was growing in thin, straggling arches, curving over at 9 to 10 feet from the ground, with such open space below that most ungulates could have got through; leafy along the arches, with much fruiting but little germination. Elsewhere, however, in ring-barked miombo, most of the *Caesalpinia* had died out at an arch height of 6 to 8 feet. *Rhus glaucescens*, 9 feet high, excellently healthy, dense, leafy and green. *Nerium oleander*, pit planting, good, 6 feet high, overhead trees ring-barked.

6.—CONCLUSIONS DRAWN FROM THE PLANTINGS.

(a) The plantings in the *swynnertoni–pallidipes* belt in Shinyanga.

While a number of species are succeeding as the outcome of perseverance in experimentation against a most difficult climate, two stand out from the rest. These are Ceara rubber (*Manihot Glaziovii*) and manyara (*Euphorbia Tirucalli*). The first not only survives difficult conditions and can be sown *in situ*, but regenerates early and well, throws its seeds far and forms thicket. The second, with its ready growth from cuttings planted *in situ* in drought and its very dense evergreen foliage, is ideal as a fly barrier.

Of *Eucalyptus*, *Cupressus*, *Callitris*, and *Pinus*, the last three have failed to withstand the conditions, the first to withstand the termites. *Cassia siamea* can be successfully sown where it is to grow, with some luck with the weather and, even then, some re-sowing. As a clean-stemmed tree that, under Shinyanga conditions, rather discourages thicket, it would probably only be useful if planted to a depth of some miles.

As neither Ceara rubber nor the manyara are nowadays of economic importance it is cheapest and probably simplest, under Shinyanga conditions, to trust to a broad width of country enthicketed by protection from fire and to fill only the larger flaws in the thicket with the two species mentioned.

Of the climbers, *Harrisonia abyssinica* is the best.

(b) The plantings in the *morsitans* belt at Itundwe.

Eucalypts, which in very broad bands might be useful, are much too liable, sooner or later, to wholesale damage by termites to be worth planting. The same applies to *Hakea suaveolens*. *Cassia didymobotrya* and *Dodonaea* (both natives) are proving (it would seem) too short-lived. *Rhus glaucescens* (native) is really better than *R. lancia* (introduced) owing to its closer habit, but is slow-growing. *Harrisonia* (native) is excellent. *Caesalpinia* (introduced and flourishing in Arusha) does not everywhere stand the Itundwe conditions. *Cassia siamea* would probably be excellent everywhere if given an unhampered start, but it makes timber not thicket, though under Tanga conditions natural thicket grows up below it. *Schinus molle* is good in the "*Acacia spirocarpa*" conditions, but older trees are now failing on the granite soil of the homestead. *Leucaena glauca* is good but scraggy, and in any case is unusable unless protected from antelopes.

The outstanding point is the general excellent health of the two conifers *Cupressus arizonica* and *Callitris robusta* or *calcarata* despite intensive competition by tall grass and *Solanum*, which has certainly brought down the height. They were nibbled back, but to nothing like the same extent as *Leucaena*. Under proper plantation conditions they would have made a very good showing and they are calculated, under such conditions, to make a very fine barrier against tsetse. Such plantations would in any case be fenced.

7.—INDIGENOUS AND EXOTIC SPECIES RESPECTIVELY.

A trouble with most native savanna trees and shrubs is that their early growth is excessively slow. They spend in some cases years in building up a thick root, and only when thus insured against death from drought and grass fires do they venture upward. *Kigelia aethiopica* is apparently an exception and there may be others. The rule does not apply to plants with their roots already established, hence the rapid growth of thicket which follows the exclusion of grass fires. Hence also the suitability for our purpose of *Harrisonia*, which, where it grows, is often so common that a large stock of well-rooted plants can be brought in from the bush.

8.—BARRIERS OF PLANTS OF ECONOMIC VALUE.

The question has long been considered whether trees or shrubs of economic value might not be included in our barriers to repay their cost later on, and a number have been tried, such as Conifers, *Fourcroya*, and *Anatto*. It has been regretted also that no economic use, such as essential oil or paper pulp, could be found for the *Lantana*, thoughtlessly introduced years ago, a pest now in certain districts and a possibility as a barrier against tsetse under fair rainfall conditions. Amongst timber trees *Cupressus* and, in their early stages, Australian Blockwood (*Acacia melonoxylon*), and some of the Eucalypts (such as *E. microcorys*) make a dense enough thicket below for the purpose in those districts with better rainfall in which they will grow at all. *Cupressus* is the best, as long retaining a dense lower growth. *C. arizonica* and *Callitris robusta*,

both regarded as drought-resistant, have failed to survive Shinyanga conditions, but as will have been seen, have done well under what are probably average conditions for a *morsitans* fly belt. Likely Conifers of these types deserve trial from our point of view wherever, through the proximity of a railway and a future demand for such timber, strips of them could be exploited, while other strips, behind those felled, would be still coming on and impenetrable.

Probably any closely planted timber—Eucalypts, Conifers, *Cassia*—in sufficient width and fenced against game, would form a barrier, for the *morsitans* group at least does not favour homogeneous wooding. One must remember that in the Tanga hinterland (see sub-section on man-made fly belts, p. 175 above), where large rubber and *Cassia* plantations, full of undergrowth, harbour the heavy-wooding flies, these plantations are merely islands in much open and semi-open country. The barrier must be continuous, and fencing against passage of game will be necessary, but the width might still have to be great to prevent hungry tsetses from passing it in numbers sufficient to establish a colony beyond.

All this wants testing—on all species of tsetse—and with the extension of the activities of the Forest Department which one still hopes may some day come, some fine projects might be attempted for the combining of the confinement of certain tsetses to the tracts that they are in with the provision of the timber of the future.

9.—COUNTRY WHICH IS, AND WHICH IS NOT, SUITED TO THE FORMATION OF NATURAL THICKET BARRIERS.

It would seem that the Itigi type of thicket (on which *see* pp. 307–315 above) could not be reproduced at all fully except on the Itigi duricrust; but other soils have their thicket types also that potentially are not less useful than that of Itigi. What country will and will not produce suitable thicket with some rapidity can only be determined by someone who knows the plants and their ecology and also the fly problem thoroughly. Broadly speaking, thorn country (*Acacia–Commiphora*). except on wet mbuga and extreme hard-pan, goes to thicket much more readily than miombo (*Isoberlinia-Brachystegia*). In parts the latter also turns to thicket fairly easily, or (under more humid conditions, as at Kwale and on the middle Wame river in Kilosa) may even be found combined with what amounts to rain-forest undergrowth. In other parts (as in Kazikazi) it seems that it never can support thicket. This may possibly be partly the result of a divorce from a thicket-forming seed-supply suited to the conditions, but it is probably still more the consequence of the competition of the *Isoberlinia–Brachystegia* trees under conditions that will not support both trees and undergrowth. Similar competition seems to be very effective and exclusive in the woods of Mopane (*Copaifera mopane*) in Rhodesia. It is seeming more and more probable, however, that over certain large areas *Isoberlinia-Brachystegia* will, even if slowly, turn to dense thicket, either of shrubs or of saplings.

10.—THE EFFECT OF THE DECIDUOUS THICKET AND EVERGREEN BARRIER IN SHINYANGA IN PROTECTING A ROAD AFTER A PERIOD OF FIVE YEARS.

The actual experiment to test the above was devised and carried out by Vicars-Harris, and I quote from his report. The course of the experiment lay from the beginning of the bush at the north-east point of the junction of Blocks 4A and 4B south-westwards down each side of the thicket barrier (*see* map 2) to the Ningwha river. It will be remembered that 1,365 yards of this barrier are

of deciduous thicket produced by not burning the grass and the remaining 1·74 miles of the evergreen shrub *Euphorbia Tirucalli*, still with weak points in it.

Each of the two parties of catchers consisted of three boys and a screen. The right-hand party went each day down the road and the left-hand party down the fire-break running parallel with the road and just on the other side of the thicket barrier. The road party, having fewer flies to catch, forged ahead of the other and so "obviated the objection that the inside party might be catching the flies before they had time to cross the barrier or find a way through."

TABLE 51.

A comparison between the flies found on the infested and protected sides of a narrow thicket-barrier.

1. Along the fire-break on the infested side.

Date	*G. swynnertoni*			*G. pallidipes*		
	Males	Females	Total	Males	Females	Total
5.i.35	33	2	35	3	—	3
12.i.35	31	2	33	2	—	2
18.i.35	34	—	34	1	—	1
1.ii.35	32	2	34	—	—	—
14.ii.35	55	10	65	2	1	3
23.ii.35	28	2	30	1	—	1
2.iii.35	31	2	33	—	—	—
23.iii.35	14	3	17	—	—	—

2. Along the road on the protected side.

Date	*G. swynnertoni*			*G. pallidipes*		
	Males	Females	Total	Males	Females	Total
5.i.35	2	2	4	—	—	—
12.i.35	2	1	3	2	1	3
18.i.35	3	1	4	7	1	8
1.ii.35	4	1	5	2	—	2
14.ii.35	3	1	4	1	—	1
23.ii.35	3	1	4	—	2	2
2.iii.35	5	—	5	4	2	6
23.iii.35	10	1	11	7	3	10

The rise on the last day was believed to be due to passage of flies on game.

From the above it will be seen that even if we suppose that all the *G. swynnertoni* caught on the road had previously come through the barrier, they amounted only to 11·59 per cent. of the flies caught beyond it. This was in spite of the fact that a road is a great attractant to tsetse, as this road was itself before the formation of the barrier, and the further fact that game passes the *Euphorbia* freely, even game-paths having been formed through it by the smaller ungulates and carnivora. Actually it is probable that many of the flies came from Block 4A, and an experiment with marked flies will be carried out to test the possibility.

G. pallidipes is very different. All past evidence has gone to show that it is a bold and enterprising fly and actually twice as many of these flies were caught on the road as off it.

E.—HUMAN ACTIVITIES AS A FLY BARRIER.

In the case of *G. morsitans* it would seem that something far short of the extermination of the bush, and far short of the extermination of the game, may hold up an advance or produce a retreat of the flies.

Several times it has happened that natives have been brought into a spot to carry out work, and the flies, abundant up to the moment of their arrival, have almost disappeared when the contingent has built its camp and begun its work of clearing, long before this last has gone far. Jackson placed his camp at Kakoma in a fairly dense fly area, for the sake of easy experimentation. The general habits of the game animals were, he reported, unaffected. They were not molested and they drank openly and freely at the waters close to the camp, though some hartebeests that came there departed. Bush was not cleared. But the flies soon diminished to such an extent that the experiments now are in danger. Nash found something not dissimilar happening when the ecological rounds were being laid out at Kikore.

Lamborn's defence against an advance of *G. morsitans* in Nyasaland appears to have produced a striking example of the phenomenon here referred to.* The original clearing † was inadequate to stop an advance of *G. morsitans* and the flies swiftly crossed it in some numbers. Lamborn bought up in support certain tobacco interests. These consisted in Europeans who in addition to growing tobacco themselves induced natives to come in and settle and grow it, and to sell the product to themselves. The result, shown to me by Lamborn, was a number of small tobacco and food gardens scattered freely through miombo wooding that was otherwise well-grown and uncut—to a total depth of about 4 miles on two dangerous sections of the front. There was frequent passage of man through the uncut strips between gardens. Game hunting was permitted and took place both on the part of the Europeans in charge and of the native tobacco growers, but, so far as the latter were concerned, it was only intensive during the time of the grass fires, and, as the spoor showed well towards the close of this period, in October, a modicum of game remained present right up to the settled strip and it was still quite abundant just outside it. Yet the flies that had crossed disappeared and a withdrawal of the invading fly population from the neighbourhood of the partially settled areas has taken place also.

One or two other factors may be present. Thus on much of the front there is a change of the wooding at the barrier line itself from miombo to *Pterocarpus–Combretum*, regarded by us as less suited as a permanent habitat for *G. morsitans*; but this is by no means on the whole of the front. Again, there is a history of the flies having once before reached this limit and retreated therefrom. And it is good grass-burning country and Lamborn used grass fires. But the line was well chosen and I feel that on certain parts of it that could have been crossed Lamborn has shown us a relatively cheap contributory method of stopping an advance by *G. morsitans* where natives for settlement are available. It is a method, at least, that is well worth testing further. That a localised and incomplete effect on the habits of the game was part of the cause is fairly certain.

G. swynnertoni does not thus retreat from contact with man, nor apparently (*see* p. 176) does *G. pallidipes*. Settlement has proved actually deleterious in relation to *G. swynnertoni* when clearings were narrow.

* Addendum in 1935, after my visit to Nyasaland.

† *See* fig. 2.

F.—OTHER POSSIBLE FLY BARRIERS.

1.—THE DOUBLE GAME FENCE IN SOUTHERN RHODESIA AGAINST *G. MORSITANS*.

The Rhodesian barrier is of two parallel barbed-wire fences from 10 to 20 miles apart, the miombo wooding being left standing between undisturbed, but the food-animals (game) inside being exterminated by an organisation of rangers in the employ of the government, with native shooters assisting them.

The Rhodesian barrier in the narrower widths seemed not altogether satisfactory at the time of my visit in 1932, owing to the infiltration of flies that was taking place across the ten-mile barrier near Gatooma. This was happening even with game-destruction so advanced that the shooters had great difficulty in finding animals, those that remained having become highly nocturnal. It was thought advisable by the Chief Entomologist to increase the width to 20 miles between fences and this had been done already in Lomagundi. The broader barrier was producing better results and has since been definitely successful in stopping the serious fly advance across which it was thrown, and even in causing a recession (Jack, 1934, and p. 226 of the present paper).

2.—WATER.

It is known that *G. palpalis* will cross widths of 400 yards between islands, and indirect observation suggests that much greater width will not be crossed. The maximum width which, combined with varying degrees of conspicuousness in the target, will be crossed has yet to be ascertained. The last factor is probably important.

3.—ESCARPMENTS.

The effect of these appears to vary with circumstances. I have seen escarpments in Portuguese East Africa and Mkalama, which appeared to be continuously effective. On the other hand, flies were ascending the Zambesi scarp in the Darwin District of Southern Rhodesia, probably carried, and the Rift scarp in Singida does not appear likely to be fly-proof. Here again further work is required.

4.—A VERTICAL WALL.

The possibility of a vertical barrier was referred to in my annual report for the year ending March 1930 (p. 20). Tsetse flies mostly fly low and settle much on the ground, and Mr. Burtt's experiment, referred to on p. 312 above, suggests that they do not normally fly over any great width of thicket. It is possible, though unlikely, that a 20-foot fence of corrugated iron or smooth other material might stop their passage, especially if painted white. It is true that a grass fire might drive them over, or they might work up to the top as they do on the outside plants of a thicket. Material cheap enough for the purpose would be the difficulty, for the corrugated iron that would be required for one mile only would cost in Shinyanga £580, quite apart from the labour and the cost of the very strong framework required. Capt. C. Y. Stevenson, Director of Public Works, Tanganyika, informed me that the mere framework of the palm-leaf screen round the tennis courts at Dar-es-Salaam cost £180 per 100 yards.

A first small experiment in this connection took place in the room of a roofless house at Shinyanga. The high walls were evenly whitewashed and the place of the roof was taken by white mosquito netting. Two hundred flies, nearly all

recently fed, were released and, despite the white colour of the walls, flew straight up to the apparent opening above as they would if they were placed in a Harris trap. The flies had been crowded in small gauze cages, buzzing to escape, and on being released within four inhospitable white walls, at once tried to escape. A similar release of crowded flies by Jackson against a dense narrow brush-barrier in Kazikazi led to a similar result, the opposite of Burtt's findings from his experiment under natural conditions (*see* p. 312 above). I regard such releases of confined and deranged flies as being not necessarily reliable.

It is probable, however, that for a mere wall to have the least chance of success it would have to be topped right along with a width of wire-gauze, against which the flies would impinge. The top margin being turned over they would probably buzz up it till they got to the fold, then buzz down again as they regularly do in the guard of a Jackson trap. It may just be worth an experiment, but, as stated already, the expense of a barrier of this kind is likely to be prohibitive even if it could succeed.

G.—THE GAME BARRIER EXPERIMENTS, SHINYANGA.

1.—PALISADES OF LIVE POSTS.

While parts of the old *Commiphora* palisade still look flourishing and nearly all the surviving posts have thrown out long branches, the termites continually take one pole here and two or three there, and generally the poles have become spaced. No really useful measure of protection from termites has come out of our experiments to this end, and, splendid as *Commiphora* is for an antelope fence where termites are not abundant, it must be pronounced useless where they are, except as a close, strong and conspicuous support for wire. Even the filling in of every small gap in three miles of the *Commiphora* fence for the carrying out of the passage experiment described on p. 300 above proved expensive. *See* Section 3 below.

Of other species grown from truncheons, *Jatropha curcas* and *Gliricidia maculata* have been discarded as too liable to termite attack. *Euphorbia bilocularis* may be useful. *Synadenium Grantii*, with particularly acrid latex, is finding Shinyanga trying and is liable to damage by wind.

Of species sown *in situ* to make a live palisade it has been impossible to get a continuous fence of *Cassia siamea* owing to the adverse Shinyanga conditions. *Moringa pterygosperma* (first recommended to me by Mr. A. J. Wakefield, Deputy Director of Agriculture), judging from the prowess of lucky individuals, would be excellent if it could get a good season to start it. The seeds are large, the germination satisfactory, and the growth extraordinarily rapid. It does not make so large a tree ultimately that the dwarfing of many individuals is likely to be a strong feature as with *Cassia siamea*, yet it makes a sufficiently thick stem to counteract somewhat the " cabbagy " quality of its wood. No fence will keep elephants out, but close-planted *Moringa* with two or three wires might suffice against ordinary antelope. It is said also to grow readily from truncheons. *Markhamia platycalyx* (Msambya), seed from Ukara Island, used in Uganda for live fences, has survived unexpectedly well and under rather better conditions it should be useful. *Manihot Glaziovii* (Ceara rubber), which elsewhere is sometimes grown as a fence from seeds or from truncheons was suggested by the Director of Agriculture. This has now been planted, stands the conditions excellently, and will be tested further. For Shinyanga, wire will be necessary for reinforcement of a palisade fence. A row or rows

of one of the small dense agaves along the foot of the fence might be added were it wished to discourage dikdiks. Giraffes are admittedly a difficulty. In Shinyanga they blunder through or fall over our *Commiphora* palisade, but the poles of the latter being still quite close, their wiring might possibly suffice to discourage even the giraffe. High-slung wire cable, discarded for use in the mines, was thought of for elephants, which are easily deterred by such things, but its transport is expensive.

2.—THORNY FENCE-PLANTS.

The six-row barrier-strip of commercial sisal (*Agave sisalana*) was extended to cover various conditions of soil and rows were added of the smaller, more compact *A. vivax.* Despite preparation of the ground by ploughing and subsequent annual weeding *Agave sisalana* has done well only in places and even here in our very severe late dry season the leaves flop, wilted, on the ground. *A. vivax* is happier. Suckers of *A. sisalana* planted between the posts in the *Commiphora* palisade and helped by the shade from the latter have filled the spaces so well that it would be impossible there even for a dikdik to pass. With the yet more effective *Agave*, probably *A. vivipara*, var. *variegata*, which was figured in pl. 4, fig. 5 of the last annual report, a small start has been made, but the nearest available supply is near the coast and we have not been in a position to repeat the expenditure on railway charges that we incurred on a truck-load of *A. sisalana.* The Prickly Pear, which in country that is annually burned does not spread, has been added experimentally to our plants. " Mauritian thorn " (*Caesalpinia sepiaria*) struggles bravely but is gradually dying out. *Harrisonia abyssinica*, an excellent local thorny trailer, could be used in conjunction with a wire fence to climb over it and make it conspicuous. A combination of three species of *Agave* is being tested as a small experiment to obtain an idea of its possible efficacy as a " monkey-puzzler " for baboons.

The above-mentioned plants, and others of use, would do well under better conditions as regards moisture than exist in Shinyanga. Thus Mauritian thorn (*C. sepiaria*) grows wild luxuriantly in Arusha.

3.—A HARD-WOOD PALISADE.

A short fence of *Combretum* and other durable and semi-durable genera, originally felled close by but replanted very densely indeed, cost for labour Shs. 50·65 per 100 yards or about £42 12*s*. a mile.

4.—BRUSH FENCES AGAINST GAME.

Three types of brush fence have been tried. In the two best the brushwood forms a core, packed down between two lines of posts with rails wired on to them. In one the rails run parallel with the ground and twice the number of rails and of wire bindings are needed. In the other the rails form a vertical zigzag.

In this latter form the cost of labour and binding-wire was Shs. 18·82 per 100 yards or under £17 per mile. It will probably be necessary to bind the two lines of rails together at the top with wires, which will slightly add to this cost.

The advantages of this type of fence are :—(*a*) that it utilises material which is on the spot ready cut, if the fence were combined with a clearing; (*b*) that it can easily be erected by tribal and unskilled labour, under supervision; and (*c*) that it forms an immediately effective barrier.

The disadvantages are :—(*a*) that it will not be long-lived, being subject to

termite attack and decay; and (*b*) that as it dries out, it will become extremely inflammable.

Where it has actually been used by us (on the Masindi river) insurance against wholesale disaster was attempted by means of 100-yard inserts of live palisade at half-mile intervals, but this did not ultimately save the fence from a fire. As a purely temporary measure a well-made brush fence is undoubtedly a useful, if somewhat a risky, expedient.

5.—WIRE FENCING.

A fence of eight strands of wire at the rate of £70 per mile for material, railage, transport, and erection, with some brushwood along the bottom, costs in Shinyanga three times as much as the better brush fence. But a wire fence with durable posts is permanent, though its invisibility makes it specially liable to be broken by game, but (*see* p. 328 above under thorny fence-plants) this might be remedied by means of the thorny trailing *Harrisonia.*

Two or three strands of wire, twisted together or otherwise, at breast height for game animals would in any case be necessary to hold together and strengthen any palisade fence.

PART 5.—SURVEY.

A.—AERIAL SURVEY OF TSETSE SITUATIONS.

1.—THE HISTORY OF THE METHOD.

I had long been certain—if only from the recognisability of vegetation on plains as seen from mountain-tops—that aeroplanes would be most useful for the survey of vegetation which forms so inseparable a part of tsetse survey, but my exploratory flight only took place at Christmas of 1929 with Captain Hordern as pilot. Well-known country was traversed, from Babati to Kondoa-Irangi, with a swing out over the Masai steppe. It was found that all the main plant-communities were readily recognisable and that the method would certainly be invaluable.

A request to the Government for an aeroplane for the Department was preferred in 1927 and subsequently pressed. When this was finally agreed to, the arrangement—excellent initially—was that the Survey Department should have aeroplanes and should hire them to the departments requiring them, including our own.

The majority of the following aerial surveys and reconnaissances were thus carried out through the kind assistance of the Survey Department, which also undertook the photography. The later flights have been in Wilson Airways' aeroplanes. All visual and sketching reconnaissance has been conducted by members of the Tsetse Research Department, carried as observers.

2.—AERIAL SURVEYS AND RECONNAISSANCES IN THE LAKE PROVINCE.

An area of about 80 square miles in Western Shinyanga, part of the country in which we are conducting our research and our large-scale field experiments against *G. swynnertoni*, was photographed in mosaic from the air during the periods June July 1931 and January 1932. A large number of oblique photographs were taken also. Messrs. A. N. Francombe and A. M. D. Howes were the pilots, and Burtt (and later Moggridge) accompanied the flights as observer and to help with the photography. The latter was carried out by means of a Williamson Eagle Aircraft Camera. The vertical photographs were taken from a recorded elevation of 10,000 feet, *i.e.* from an elevation of about 6,000 feet above the level of the ground; obliques were taken at about 1,000 feet above the ground. Haze was troublesome and partially spoiled a great many of the photographs. The best period was January, when haze was absent and clear results were obtained apart from cloud shadows. The obliques were all good. The better results have been definitely useful and some of the photographs are reproduced in this paper.

Reconnaissance flights over Nindo, over the south-eastern and southern portions of the Huruhuru Plains, and over Block 9, inspection flights over the general area under reclamation measures in Shinyanga, over the still-combined Blocks 10B and 10C (*see* map 2) for the choice of the barrier between them, and flights to give each member of the staff a bird's-eye view of the area of his own special work, have on various occasions been made by Vicars-Harris, Potts, Burtt, Napier-Bax, Jackson, Wheeler, Moggridge, and myself, under

the pilotage of Francombe and V. W. Soltau. These flights have served the object in view in a really invaluable manner.

Reconnaissance of the outline of the eastern fly belt from Kitalala in Uduhe to Maswa, inclusive, and of the eastern belt from Smith's Sound south past Buhungukira was carried out by Potts, Napier-Bax and Vicars-Harris, with Soltau as the pilot. The object of the flights was achieved.

A flight with Soltau in April 1932 gave me a good idea of the general vegetational position in much country in which we are, or are likely to be, working. A continuation of this flight to Entebbe and a subsequent flight (in June 1932) from Entebbe to Kisumu, gave a good general idea of the vegetational interspersion in the most extensive haunt of *G. palpalis* in east Africa.

3.—AERIAL SURVEYS AND RECONNAISSANCES IN THE CENTRAL PROVINCE.

It had been found by observation that dense thicket of the type that occurs along the railway between Kazikazi and Manyoni was likely to be a barrier against tsetse. We wished to find out in what width it would be a barrier and whether the tsetses, passing narrower widths, flew over or worked their way through. It was necessary for this investigation to select thickets of relatively small but varying width for the purpose of experimentation. Kazikazi, on the edge of the great Itigi thicket system, with its bays and projections, seemed indicated, but, the country being flat, it was impossible to choose sites from the ground. An aeroplane was secured, Burtt went up, and at once found a mile-wide thicket neck, a long, two-mile wide thicket (as well as greater widths) and an island of *Isoberlinia–Brachystegia* glades, interzones and all, which was a miniature fly belt and was christened, from its shape, the "Racquet." This last was in the heart of a great barrier thicket. The map of this area, which is given in pl. 20, fig. 2, results from Burtt's sketches in the air. Photographs also were taken—a complete mosaic of the "Racquet," and others, vertical and oblique, that showed types of country and one of Burtt's thicket-barrier experiments (pl. 17, fig. 2). The pilots were Francombe and Howes. Inspection flights followed by Jackson and myself.

It was desired to map the great Itigi and Rift Valley thicket systems and to ascertain if use could still be made of any part of it as a defence against the invasion of *G. morsitans* into Singida from the west (Matelele belt) and south (Hika belt), and, particularly, to gauge how much of the Singida country was under miombo wooding and therefore threatened. It was quite certain that serious advances of fly were still taking place. It was equally certain that we might work on ground survey for a year or two years in this extensive bush country, much of it quite impossible to get about in, and would still be uncertain if we had exhausted the possibilities favouring the tsetse or assisting ourselves. It was probable that a very few days in the air would enable us to size up the whole position fairly accurately.

The programme was therefore as follows : (*a*) a preliminary reconnaissance from the air, both with the above object and for the choice of the experimental sites near Kazikazi; (*b*) ground work to fill in the distribution of the fly and decide where more knowledge was needed; and (*c*) a more detailed air reconnaissance in parts, or even air-photography, where the ground work combined with the results of the initial reconnaissance showed detailed information to be necessary.

Burtt was instructed accordingly. Jackson was to join him and fly over the Usandawe problem of Western Kondoa, of which he was in charge. An

aerodrome had been constructed by us at Kazikazi, and the three-seater Avro, "Arcturus," arrived at Manyoni on 9th September.

In the course of flights on five days, Burtt made sketches and notes from the air and produced the valuable result shown in map 6, of the present paper (*see* p. 30 above). Naturally it does not claim even a very distant approach to the accuracy of a photographic or instrumental survey, but it gives a good idea, which we had not before despite months of work, of the general distribution of the main thicket masses and of the miombo.

In the course of these flights Jackson had been picked up at Kondoa and a joint flight had been made with him over the western boundary of the Usandawe fly advance, passing over Masiliwa and Kwamtoro, the total flying hours being 6 hours and 10 minutes. Heavy cloud shadows spoilt the definition of the thickets on the 11th—so black were the shadows and on two days haze made observations difficult. On the 15th the coming off of a cylinder-head might have produced disaster, but, losing height all the time on a 30-mile retreat to the Kazikazi aerodrome, the aeroplane reached the latter none too soon. The work, however, had to cease.

It had been clear from this survey (*a*) that the threat to the remains of Singida and to south Mkalama was exceedingly serious, there being miombo everywhere ahead of the fly advances; and (*b*) that the great thicket still divided the western (Matelele) advance from the eastern and southern, and that there were broken lines of " island " thickets clothing rises in the Usandawe country which might be of use in defence. Two types of thicket were distinguishable—*Commiphora–Grewia* thicket and the Itigi type.

I made an inspection flight through the length of the area followed in November, and was able fully to confirm Burtt's view as to the very great seriousness of the position. I was struck incidentally with the clearness with which the leafless thicket, nearly black from the air, showed up, and with the distinguishability also even of the leafless miombo, showing silvery grey.

Again, we wanted to ascertain why the fly was not advancing on the Kisigo river front in South Manyoni, it being quite certain that the narrow and incompletely cleared settlement that had been put in there could have no effect on the invasion.

The result is given on map 6. A wide belt of thorn-bush and other elements unsuited to serious invasion by *G. morsitans* is continuous betwixt thicket and thicket, along practically the whole front. The view as to the inadequacy of the settlement was very completely confirmed.

A reconnaissance flight was also undertaken by the Botanist on 6th March, 1933, accompanying the Director of Veterinary Services, in connection with the stock route from Kondoa–Irangi to Korogwe, for the purpose of ascertaining the position along the route as regards grazing, water, and the possibility of protecting its fly-infested or fly-threatened sections.

In planning the withdrawal of the outlying Singida settlements into a more central distribution as a protective measure against sleeping sickness in face of *G. morsitans* advancing from three sides at once, Dr. Maclean laid out on the ground provisionally a hexagon (shown in map 6) within the periphery of which it was calculated that the population could be contained. He asked that the Botanist should be lent to make a survey of the distribution of the woodland communities along the lines of this hexagon. An aerial sketch map was accordingly made of the distribution of the woodland types crossing these lines. The main point of importance resulting was the discovery of a thicket area between Singida and the Hika advance which, it is possible, can be utilised as part of the defence.

4.—THE VALUE OF AEROPLANES IN TSETSE WORK.

(a) Advantages and disadvantages of visual reconnaissance.

Flying at 3,000 feet above ground-level even individual trees can largely be recognised if in leaf and every detail relevant to the control of tsetse through the vegetation stands out most clearly—" every island of bush in the great open mbugas, every mbuga and glade in the greater bush areas, bridges of bush connecting bush areas, lines along which barrier clearings could most cheaply be made, distribution of thicket, probable sites of fly feeding-grounds, rocky outcrops which might be breeding-places, nature of the soil in some cases [in most cases by inference from the vegetation], situation of waters, villages, paths " (Swynnerton, March 1930, Annual Report on Reclamation). This was in the leafy season—in December.

" In our air reconnaissance in the Central Province, at 7,000 feet the main types of woodland could be distinguished; and thicket dense or more open. From 10,000 feet the effect was in a way better, provided visibility was good; it was a smaller scale map, and it was possible to take in better in its entirety each area of particular type and its relation to other areas. Three flights, costing £15 9*s*. 0*d*., or £3 2*s*. 0*d*. per hour, or 78 cents per mile, seemed to tell us fairly completely how far and where we could rely on major natural features to assist us in defending the districts of Singida and Manyoni from the fly. Not much small detail could be recorded, but this would come later with air photography in selected sections in a suitable month of the year." This was written in relation to flights in September and November. As a broad survey this work was invaluable, even under dry-season limitations.

The above reconnaissances would have taken us many months on foot and we could not have been sure even then, in this great, continuous bush area, that we had not overlooked much that might have assisted or that might yet defeat our defence. The mind cannot assimilate much of the detail seen during a flight, nor can such small detail as we need for attack on the fly be sketched at all fully unless the ground in question be flown over several times. It is here that photography is useful. Every small detail is placed on record for all time, for the use of others beside the observer, vastly more fully and accurately than in any sort of a sketch, and in a form in which it can be studied with a stereoscope.

(b) Vertical *versus* oblique photographs.

Vertical photographs, well taken, are ideal, but the method is very expensive and the close detail is not everywhere needed. Visual reconnaissance, with note-taking and sketching, combined in parts with oblique photography, would meet most of our needs, but vertical photography would be best for a few " key " situations.

(c) General limitations and difficulties.

At 5,000 feet it is difficult or impossible to see small wooding of the *Acacia Stuhlmannii* or gall-acacia type in the leafless season, especially with haze present, or to identify leafless trees except baobabs. On the other hand, when conducting mere visual reconnaissance one can always come down lower to inspect. In the dry season the following air-note was made over thorn-bush in Shinyanga. " At 2,200 feet: *Baobabs*—vertically like spiders with curly legs, visible far better obliquely; *Acacias*—all visible as small round grey blobs against yellow grass; *Commiphoras*—small spiders—like the baobabs but smaller and mostly quite indistinguishable."

The indications offered by the different grasses are important. The longer grasses have a stippled appearance; hard-pan grass is perfectly smooth in grain. Other indications of conditions will be present to anyone knowing the vegetation locally at the moment. Thus in July 1931 Burtt noted the presence of seasonal ponds, now dry, through red-brown patches produced by the swamp plant *Hygrophila spinosa*, while rather different red-brown patches near cultivation indicated *Sphaeranthus indicus*. That to persons unpractised in the air, though knowing the plants, even trees in leaf may prove deceptive, was illustrated by a flight by two entomologists over Nindo on which extensive and close *Acacia Fischeri* was mistaken for miombo in leaf.

In vertical photography invisibility of the types referred to above as hard to see, and especially of small, leafless *Combretum* and *Commiphora*, occurs also and is more serious.

In the Shinyanga photographs taken with some dry-season haze present, of the four highly important bush-types of which we wished to ascertain the exact distribution only one can be seen at all fully. Two types (*Commiphora Fischeri* and *C. Schimperi*), with light-branching crowns, cannot be detected at all against the grass though covering extensive areas; a third (*Acacia* spp.) with densely-twigged crowns, also extensive in range, can only be clearly seen where odd trees still keep their leaf. Of the rest of the Acacias perhaps 20 per cent. show as ghosts not readily distinguishable from shadows that occur in the grass in quite open areas; the others not at all. Even the smallest shrub that remains in leaf is highly visible, but large trees and whole groups and woods of trees cannot be seen at all—even in the 3,000-feet photographs. But the way in which the different grass-types show up (both in verticals and obliques) may be seen in pl. 12, fig. 3.

In the oblique photographs, taken at any time, it has been easier to identify trees, though their detailed utility in this respect ceases at under a mile.

(d) The best time of year at which to take aerial vegetational photographs.

The conclusion was reached that the long dry season, late June and July, when the above notes were taken, was not a good time for air photography for our purpose. On the other hand, the photographs show up at least four types of grass; such types are connected as a rule with one woodland type or another and the length to which a grass grows is important in relation to tsetse-fly feeding-grounds. September was much too hazy.

In the early rains, November was good. Soon after the trees come into full leaf would in any case be an excellent time, as there is then the differentiation in tint that one gets again in late May. Early December should do; but the date varies with the year and so does the incidence of the rains, while much cloud will certainly be present. In a December photograph the bush will show up but the grass will show small differentiation. In the short dry season, January and February combine the desiderata of a break in rains, bush in leaf, though more uniform, and grasses in flower and differentiable.

During the long rains cloud shadows make photography impossible, but when they come to end, early May (grass in seed, bush not yet leafless) is useful, though cloud shadows are still somewhat troublesome; late May is good and shows differentiation in leaf-fall. A difficulty in or near the rains lies in the clouds. Waiting for a day with few clouds has wasted days at a time. Here the presence of a resident government air-survey organisation, which, failing to complete at one visit, could be called in for another attempt, has been useful. Haze is less of an impediment to oblique, than to vertical, photography.

B.—SURVEYS, RE-SURVEYS, AND BRIEFER RECONNAISSANCES CARRIED OUT ON FOOT AND BY CAR.

1.—SURVEYS CARRIED OUT IN THE PERIOD 1931–34.

The following table contains a list of the surveys carried out on foot or by car in Tanganyika in the period 1931–34 by members of the Tsetse Research Department.

TABLE 52.

List of surveys carried out in the period 1931–34.

S = Survey.
FS = Very full survey.
ES = Entomological survey.
R = Reconnaissance, brief or prolonged.
RA = Reconnaissance, or inspection, for approval or advice.
FRS = Formulation of reclamation schemes.

A very small number of our earlier surveys are included for their historical interest.

Survey, reconnaissance or inspection	Officer concerned, nature of work and date	Object and subsequent action
	(a) *In the Lake Province.*	
(i) North Mara	Jackson, 1934 (S).	For Administration. Action not recommended.
(ii) Musoma District generally	Jackson, 1933 (FS).	For Sleeping Sickness Officer and our information.
(iii) Banagi on the Serengeti Plains, Musoma Dist.	Swynnerton, 1933 (R).	Information.
(iv) Msalala, Mwanza Dist.	Napier-Bax, 1934 (S and FRS).	For Administration. Reclamation followed.
(v) Buhungukira, Kwimba Dist.	Swedi, 1923; Potts and Swynnerton, 1932 (S and FRS); Potts and Lloyd, 1933 (ES); Findlay, 1933 (FS); Vicars-Harris and Napier-Bax (inspection of work and further detail), 1934.	For Administration. Reclamation followed.
(vi) East Usmao and Ndagalo, Kwimba Dist.	Vicars-Harris, 1934 (R and FRS); Potts, 1934 (ES).	For Administration. Reclamation followed.
(vii) Ntukusa mbuga, Kwimba Dist.	Swynnerton, 1923 (R); Vicars-Harris, 1934 (R and FRS).	For Administration. Preliminary to reclamation.
(viii) Wida mbuga and Dasina promontory, Maswa	Moore (R) and Teare (FRS), 1926–29; Vicars-Harris, 1934 (renewed S and FRS).	For Administration. Reclamation followed.
(ix) Fire-exclusion area, Maswa	Vicars-Harris (R and marking of fly rounds), 1934; Potts (ES and marking of fly rounds), 1934; Wheeler.	Experiment and reclamation.
(x) Ntusu, Maswa	Vicars-Harris (R and FRS); Potts, (ES), 1934.	Preliminary to reclamation.
(xi) Marialuguru, Maswa	Napier-Bax, 1931–32 (FS and FRS); Swynnerton, 1932 (RA); Potts and Lloyd, 1933 (further ES and fly rounds); Moggridge, 1933 (FS, extension of surveys and FRS); Vicars-Harris, 1934 (Inspection).	For Administration and Ranch. Reclamation followed.
(xii) The Huruhuru Plains, N.W. Shinyanga	Findlay, 1931 (FS, incl. ES); Napier-Bax, 1934 (extension of surveys and FRS); Potts, 1933 (ES); Vicars-Harris, Lloyd and Moggridge, 1933–34.	Opening up grazing grounds. Full reclamation followed.
(xiii) Nindo, W. Shinyanga	Swynnerton 1923 (R); Moggridge, 1934 (S).	Information on *G. pallidipes.*
(xiv) Problems and schemes in the experimental area, W. Shinyanga	Swynnerton, Teare, Magnay, Smith, 1922–28 (FS). Practically all administrative, scientific and field members of the Department on numerous occasions since, over years.	Information and as preliminary to experiments and reclamation. Reclamation in most cases followed.
(xv) Manonga mbuga system of S. Shinyanga	Moggridge, 1933 (S and reclam.).	Opening to cattle by means of a corridor (fig. 26).
(xvi) Mihama, in S.E. Shinyanga	Vicars-Harris, 1934 (S and FRS); Potts, 1934 (ES)	Preliminary to reclamation which followed.
(xvii) S.E. Uduhe	Teare and Smith (early); Jackson and Swynnerton, 1930 (R); Swedi, 1931 (FS); Vicars-Harris, 1934 (extended FS).	do. do. do.
(xviii) Semageti	Vicars-Harris (S and FRS); Potts (ES), 1934.	do. do. do.
(xix) Ilola in S.W. Shinyanga, Lohumbo chiefdom	Wheeler (FS and FRS), 1933.	For tribe. Reclamation followed.

TABLE 52 (*continued.*)

Survey, reconnaissance or inspection	Officer concerned, nature of work and date	Object and subsequent action
	(b) *In the Western Province.*	
(xx) Gigoma mbuga area in Kahama Dist.	Vicars-Harris and Potts, 1933 (R); Moggridge, 1933 (FS); Swynnerton, 1934 (RA).	Preliminary to reclamation in 1935. Measures followed.
(xxi) Manonga river, Nzega–Shinyanga border	Teare and Swynnerton, 1923 (S); Potts, 1925 (R); Jackson, 1931 (FS).	Preliminary to a possible defence.
(xxii) Ngurube	Jackson, 1931 (S); Swynnerton, 1931 (RA); Napier-Bax, 1934 (FRS).	Preliminary to defence, measures followed.
(xxiii) Kahama–Biharamulo–Kibondo	Swynnerton, 1934 (R).	Information and choice of experimental areas.
(xxiv) Kahama-Tabora–Igalula	Jackson, 1934 (R).	do. do. do.
(xxv) Proposed *morsitans* experimental area, Igalula–Nyahua–Meta–Ugala–Tabora	Jackson, 1934 (FS); Swynnerton, 1934 (RA).	Information and choice of experimental area for field-scale study of *G. morsitans*.
(xxvi) North Isenegeja, Kahama	Swynnerton, 1934 (R); Jackson, 1934 (S).	Information and choice of non-burning area.
	(c) *In the Central Province.*	
xxvii) Mpapwa–Tubugwe–Kidete area	Swedi, 1922 (R); Potts, 1931; (R) Swynnerton, 1932 (RA); Burtt, 1933 (FS).	Protection of the Veterinary Farm, Mpapwa. Measures followed.
(xxviii) Eastern Kondoa and Usandawe	Potts, Burtt, 1926–28 (early FS); Findlay, 1927 (FS); Jackson, 1929–34 (continuous FS and ES); Swynnerton, 1932 (RA); Napier-Bax, 1932 (S and Estimate), Burtt, 1933 (R) and 1935 (FRS); Maclean (Med.) and staff; and Currie (Agr.).	Information (study of fly advance) and defence.
(xxix) Western Singida and South Mkalama	Burtt and Montague, 1923; Burtt (FS), 1927; Harrison (FS), 1928 and on; Jackson, 1934 (FRS); Napier-Bax (estimate); Phillips, 1928 (RA); Swynnerton, 1925 and 1934 (RA); Maclean (Med.) and staff; Currie (Agr.).	do. do. do.
(xxx) North-eastern Singida	J. S. Armstrong, Medical (S); Jackson, 1932 (S); Swynnerton, 1932 (RA).	do. do. do.
(xxxi) Hika fly advance from Manyoni Dist.	Burtt, 1931 (FRS).	For defence. Study of Hika–Saranda fly advance northward.
(xxxii) Kazikazi	Burtt with Harrison, 1931 (FRS; also air and botanical) (RA).	Vegetation in relation to *G. morsitans* and experiments in passage of thicket.
(xxxiii) The great mbuga dividing Masailand from Kondoa	Nash; Findlay, various dates.	Opening up grazing.
	(d) *In the Northern Province.*	
(xxxiv) The Basotu Lake fly advance	Potts, 1927 and 1930 (R); Vicars-Harris, 1930 (R); Gordon-Russell, in several years (FS); Swynnerton, 1931 (RA).	Defence. Clearings followed.
(xxxv) Yaida river	Gordon-Russell (S); Swynnerton, 1934 (R); Findlay, 1934 (R).	Preliminary to possible reclamation.
(xxxvi) Kiratu-Oldeani	Gordon-Russell (FS); Swynnerton, 1932 (visit).	Reclamation by Tully, Gordon-Russell and Administration.
(xxxvii) Ndereda–Babati	do. do. do.	For defence. Clearing by Gordon-Russell and Administration.
(xxxviii) Ufiome-Kikore	Nash and Findlay (FS and ES), 1928-31; Swynnerton, 1929 (RA); Gordon-Russell (clearing); Findlay, 1934 (FS).	For defence and reclamation. Two clearings made.
(xxxix) Masagoloda	Gordon-Russell, earlier; Findlay, 1934 (ES).	For defence and reclamation. Action not recommended.
(xl) Rau Forest, Moshi Dist.	Moggridge, 1934 (R).	Information on *G. pallidipes*.

TABLE 52 (*continued*).

Survey, reconnaissance or inspection	Officer concerned, nature of work and date	Object and subsequent action
	(e) *In the Tanga Province.*	
(xli) North-west Handeni	Burtt, 1933 (FS).	For Administration, preliminary to reclamation, which followed.
(xlii) Handeni generally	Swynnerton, 1934 (R); Swedi, 1934 (FS).	For Administration. Preliminary to possible reclamation as a measure against famine.
(xliii) Tongwe–Kiwanda area, Korogwe Dist.	Moggridge, 1934 (R).	Information on *G. pallidipes*.
(xliv) Mkwaja in Pangani Dist.	Moggridge, 1934 (FS).	Preliminary to reclamation. Measures recommended, but reclamation not yet initiated.
	(f) *In the Eastern Province.*	
(xlv) Dar-es-Salaam–Utete–Mohoro	Swynnerton, 1932 (R).	Information and material.
(xlvi) South Kilosa	Swynnerton and Bishopp, 1921 and subsequently (FS); Swynnerton, 1932 (R).	Information and (1932) fly rounds.
(xlvii) North Kilosa	Swynnerton and Bishopp, 1921 and subsequently (FS); Swynnerton, 1934 (R).	do.
(xlviii) The *G. pallidipes* situation in Dar-es-Salaam township	Medical and Veterinary Authorities (discovery 1932, and measures, 1934); Swynnerton, 1932 (RA).	Reclamation followed.
	(g) *In Kenya Colony.*	
(xlix) Maboko Island	C. B. Symes (Kenya Med. Ent.) and Swynnerton, May 1932 (FS and subsequent visits by both); Jackson, 1932 (ES and subsequent visits); Potts, 1933 (visit); Lloyd, 1934 (visits).	Preliminary to reclamation by trapping.
(l) Kuja river	Swynnerton and Symes, 1931–32 (RA); Symes and Vane (FS and reclamation).	Preliminary to reclamation which followed.
(li) Lambwe Valley	Swynnerton, 1932 (RA) with E. A. Lewis (Vet. Ent., Kenya); Lewis subsequently (S or FS); Blunt, under Lewis (FS), 1934.	do. do. do.
(lii) Kwale	Swynnerton, 1932 (RA); Moggridge, 1934 (FS).	Information on *G. pallidipes* and possible reclamation.
(liii) Kilifi	Swynnerton, 1932 (inspection); Moggridge, 1934 (FRS).	Information and installation of long investigation.
	(h) *In Uganda Protectorate.*	
(liv) Ankole	Swynnerton, 1932; Potts, 1933; Burtt, 1930; Jackson, 1932 (visits).	Information and consultation, work of Uganda Veterinary Department.
(lv) Lango	Jackson, 1932 (RA).	By request, study of the fly situation.
(lvi) C. W. Chorley's work on Nsadzi and other islands	Swynnerton, 1932;* Jackson, 1932 (visits).	Information and consultation.

2.—DESCRIPTION OF THE SURVEYS CARRIED OUT.

Of the above surveys and inspections, those of Maboko, South Kavirondo, and Ankole are described in Part 7 of the present paper. West Shinyanga, south-east Shinyanga, Buhungukira, Marialuguru, Mwanza, Huruhuru, Ngurube, Ufiome, Babati, Inchi Mpya, and the other great plains broken into, and the various surveys in Maswa, were associated with practical measures in Tanganyika and are discussed in Part 6, under reclamation. The miniature *pallidipes* fly belt in Dar-es-Salaam has been described under *G. pallidipes*. Mpapwa is dealt with partly under each heading. Other surveys (Usandawe,

Singida, North Manyoni, Basotu) concern important advances by the tsetses and will be dealt with under the sub-section "Fly Advances." Kazikazi is covered sufficiently by the section on thicket barriers. The main peculiarity of Banagi (Serengeti) has been mentioned under *G. swynnertoni* (p. 99 above). Of the surveys that remain, the more interesting are dealt with below.

3.—NORTH MARA, LAKE PROVINCE (MARCH 1934).

"This visit was undertaken at the request of the Assistant District Officer in charge of North Mara, who was worried by the presence of tsetse at a ford on the Mara river at Nyamongo, where he feared that sleeping sickness might break out.

"The tsetses present, however, proved to be *G. pallidipes* and *G. brevipalpis* only, which have never been known to carry sleeping sickness under natural conditions, and it was thus possible to say that there was no apparent danger of this disease starting there, as the nearest *G. swynnertoni* were many miles away." It must be remembered, however, that Dr. Corson has evidence which suggests that *G. pallidipes* is particularly capable of carrying the trypanosomes of the *brucei* group.

"While in North Mara, opportunity was taken to see another belt of *G. brevipalpis* and *G. pallidipes* lying between Tarimi (the Administrative centre) and Shirati on the lake. The wooding was largely of the tree Combretums with heavy wooding on the rivers. It looked well suited to *morsitans* also" (Jackson's report).

4.—THE MUSOMA DISTRICT, LAKE PROVINCE (JULY OCTOBER 1933).

This survey was carried out by Jackson at the instance of Dr. Maclean, Sleeping Sickness Officer, who feared that the belt of *G. swynnertoni* surrounding Musoma might be gradually encroaching on the settled areas, and that this tsetse, with *G. pallidipes* and *G. brevipalpis*, might eventually occupy the whole of the present fly-free area. The following is an extract from Jackson's report :—

"Musoma, standing on the south side of Mara Bay, is at present separated from the nearest *G. swynnertoni* by about 20 miles on the south side and 50 on the east. The intervening country appears at first glance to be not entirely unsuitable for occupation by this species, and some of the country quite near Musoma itself appears vegetationally perfectly suitable. *G. swynnertoni* in Musoma conveys human sleeping sickness.

"There are two principal belts of *G. swynnertoni* in south Mara, an eastern and a southern one. In the eastern belt a history of a slow and local advance into the eastern part of the Ikizu sultanate was obtained from natives round about. In the southern belt no advance was admitted by the inhabitants.

"The climate, topography, vegetation, and fauna of Musoma all differ markedly from those of Shinyanga, where *G. swynnertoni* had been previously studied, and in all these aspects the country much more resembles Ankole in southern Uganda, where the tsetse is *G. morsitans*" [though without clothing of the trees by Old Man's Beard lichen (*Usnea*) indicative of moister conditions in Ankole (C.F.M.S.)].

"As in Ankole, the principal game animals are topi and oribi; but on the plains farther out Coke's hartebeest, wildebeest, eland, roan, zebra, ostrich, giraffe, Thomson's gazelle, waterbuck, impala, wart-hog, and a few dikdik are found.

" The most characteristic tree is, again as in Ankole, *Acacia hebecladoides* locally called 'mnyenye,' growing very flat-topped as does *A. spirocarpa* farther south and in Shinyanga. Near Musoma are down-like hills, generally covered to a greater or less extent with *Combretum ternifolium*, the valleys between supporting thicketed streams bounded by *Acacia hebecladoides*. It should be noted that *Combretum ternifolium* is in drier parts of Tanganyika a tree of alluvial soils; in the moister climate of the Musoma uplands it comes out on to the hills. In many parts, compact thickets of *Rhus* sp., *Harrisonia abyssinica*, and *Grewia bicolor*, with bayonet *Sanseviera* below, are very frequent.

" As the result of these studies, it seemed unlikely that the slow Ikizu advance of this tsetse, noted above, could proceed more than another mile or so towards Musoma. On the south side of Musoma, however, the position appeared less secure, in spite of the lack of any native support for the view that an advance was occurring there. Fortunately the matter was decided by reference to a map published by the Director (Swynnerton, 1924) which showed, in 1920, a 'fly' boundary essentially identical with that at present existing.

" No measures were recommended, therefore, in the south of the area. In the east it was thought that the Ikizu advance could be left to look after itself; but on this front the tsetse had in one place appeared in small numbers in the fringe of the Unguruimi hills, although, pending retreat of the inhabitants, it could not be said to have gained a permanent footing there. The flies here had actually been crossing an open plain over an hour-glass-shaped 'bridge' of *Acacia seyal* and *Balanites aegyptiaca*. It was recommended that this bridge should be cut, and it is understood that the Musoma Administration undertook the work later. It seemed unlikely that *G. swynnertoni* would enter Unguruimi by any other route."

Points of general interest :—

" It appeared that *G. swynnertoni* avoided the *Combretum ternifolium* and affected particularly the *Acacia hebecladoides*, and that, if thicket were necessary at all, a very minimum sufficed. Moreover, thickets *without* trees interspersed failed to support this fly. Another important point was that where narrow bands of *Acacia hebecladoides* with other trees elsewhere associated with *G swynnertoni* traversed open plains (about streams, for example), they were practically fly free, and cattle could be kept. [This is the opposite of the Gigoma position (*G. morsitans*)—see below (C.F.M.S.).] Equally narrow valleys with such vegetation ascending into hills covered by *Combretum ternifolium* were uninfested with *G. swynnertoni*.

" An interesting point was that, where the advance of *G. swynnertoni* had taken place in Ikizu, near Chamliho hill (*see* map 1), *G. pallidipes* appeared to have advanced with it, as a specimen was taken in the advanced salient, from which cattle-keepers were still in process of retreat. The boundaries of *G. brevipalpis* were also apparently contained within those of *G. swynnertoni*, unless an unconfirmed report of tsetse near Buhemba should prove to be due to an isolated colony of this species " (Jackson's report).

There have been other cases in which an invasion by *G. swynnertoni* has appeared to be followed up by one by *G. pallidipes*.

5.—THE GIGOMA MBUGA, KAHAMA DISTRICT, WESTERN PROVINCE.

About five miles south-west of Kahama township, one comes out of the cultivation steppe into a part of the great area of miombo wooding which fills all western Tanganyika. A large bay of country, open through present and

past cultivation, extends into this around the chief's village of Nyandekwa. Slashing this open bay across diagonally from north-west to south-east, runs the Gigoma mbuga. It is itself clothed in its north-western portion with low, green wooding of *Combretum ternifolium* and further south with the trailing Combretums and their associates; and it contains areas of gall-acacia also. It serves as a connection between the miombo wooding to the north-west of the clearing with that on the south-east. The point of a further V-shaped mbuga enters the northern portion of the Gigoma mbuga from the north-east and miombo, again, fills the middle space of the " V."

G. morsitans (home in miombo) is the tsetse concerned and the interesting point about the situation is that, although the mbuga completely deserts the miombo wooding, in which it would normally be a feeding-ground, and runs through open country, it is kept infested by the contact of its ends and of the " V " with miombo, especially its north-east end. Moggridge carried out a full survey of the position and marked out cross-clearings at the points that would separate the mbuga from the miombo.

The main point of interest is that referred to already—that a strip of a vegetational community which, if isolated in open country, would not by itself hold *G. morsitans*, is kept infested by contact merely at its ends with the type of wooding which, to make it hospitable to the flies, must be there as its complement.

6.—THE THREAT TO THE VETERINARY HEADQUARTERS AT MPAPWA, CENTRAL PROVINCE.

(a) The general situation.

A deep valley between high hills connects the Veterinary Headquarters and Research Station at Kikombo, Mpapwa, with Tubugwe, to the east, the Station's outlying farm. A fluctuating but, on the whole, increasing number

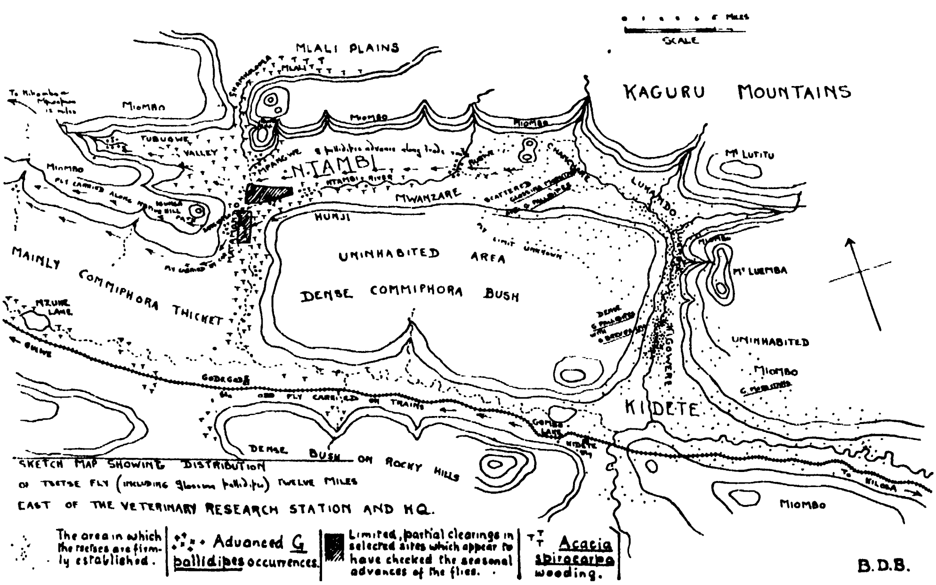


FIG. 23.—Sketch map, showing the threat to Mpapwa. The arrow in the top left-hand corner indicates the position of Mpapwa.

of cases of trypanosomiasis have taken place annually at Tubugwe, and this incidence has latterly spread to Kikombo itself, the main station. Buffalo Creek, to be mentioned later, occurs between the two but nearer the latter. Running southward and not far east of Tubugwe is a stream, called Matamondo in its course below Tubugwe. Into it from the east comes the Ntambi and its various branches. This system covers a wide piece of country and definitely connects up Tubugwe with the *pallidipes–morsitans–austeni–brevipalpis* area between Kilosa and Kidete, both these places being on the railway.

Generally speaking the upper parts of the very high hills concerned carry miombo wooding, and their low slopes dense, dry, deciduous thicket, largely of Acanthaceae. Between these and the valley bottoms scattered settlement occurs, and the rivers themselves are lined with big trees and high grass-jungle.

(b) The history of the problem.

(1) A number of flies (*G. pallidipes*) were taken by myself in May 1921 between Lukando and Kidete, near a tributary of the Ntambi. It is probable therefore that the flies then already extended in the direction of Tubugwe.

(2) The Veterinary Department's cattle at Tubugwe were shifted from the upper section of the valley, where it is more constricted, to the present site about 1924. The first cases of trypanosomiasis amongst them occurred after this.

(3) In December 1924, I sent Swedi, head fly boy, to investigate. Travelling from Kidete to Ntambi past Lukando (which he left on his right) he took odd examples of *G. pallidipes*, *G. morsitans*, and *G. austeni* most of the way. Within half an hour of Tambi village he took two flies of which the last (*G. pallidipes*) was south of west of the village.

(4) In 1927, chiefly in July and August, about 60 cases of trypanosomiasis occurred in the herds at Tubugwe.

(5) In July 1929, Potts believed that he saw a tsetse fly at Buffalo Creek in Kikombo. I accept this identification, as it is impossible that anyone who has worked much in the field with *Glossina* and has obtained a clear view could mistake anything else for a tsetse fly.

(6) In August 1930 Mr. Baird took a number of *G. pallidipes* near the village of Tambi and within one hour's walk of Tubugwe.

(7) A number of cases of trypanosomiasis occurred in the Veterinary herds at Tubugwe in 1932 and a number even in Kikombo. In October of 1932 I carried out a brief reconnaissance of the position. A fly (*G. pallidipes*) was taken on the road near the river junction towards Matamondo—perhaps not much more than half an hour south-west of Swedi's westernmost fly of 1924.

(8) Burtt in 1933 carried out surveys in both the wet season and the dry.

(c) The position as it appeared before Burtt's survey.

The evidence up to and including my reconnaissance had seemed to show that there had been no sensational advance by the flies, but that, while in some seasons they were doubtless denser than in others and threw more wanderers afield, there was probably taking place on the Ntambi river system the gradual progressive increase in numbers, despite fluctuation, which has been noted in this species elsewhere (*see* p. 108 above) and which, as suitable outlying positions are ultimately permanently held, ends in a slow but none the less sure extension of its range.

(d) The situation found by Burtt in the dry season.

(i) *Veterinary Farm, Tubugwe Valley.*

The vegetation here was characterised as follows: stream with narrow evergreen fringing forest; beside this near the Veterinary kraal a limited alluvial flat, clothed brokenly with much dense *Vernonia senegalensis* thicket eight to ten feet in height, but semi-herbaceous in appearance, grass glades between, and with scattered large trees of *Acacia albida*, *Ficus sycomorus*, and other species. Tangled *Acacia pennata–Commiphora–Disperma* dry thicket clothes the lower sides of the valley; miombo (*Isoberlinia*-*Brachystegia*) high up the slopes of the big flanking hills.

There was much spoor of buffalo in the mountains and these animals regularly came to the stream to drink and lick salt from the banks, as did the pigs. The kudus also frequently came to the salt. There were a few rhinoceros in the *Disperma*-type thickets and, in the miombo, fresh spoor of rhinoceros, greater kudu, and bushbuck (a few only); bush-pig was frequent. 176 cattle of the Veterinary herd that were present were undoubtedly frequently attacked by the flies, which were thus diverted from the catchers and prevented a full picture of the situation from being obtained.

Eight days of intensive work with three pairs of bait-cattle were spent here at the beginning of July 1933. No *G. pallidipes* were taken in the places frequented by buffalo or other game. Four were taken in all – at the cattle-dip itself, in the glades between the *Vernonia* clumps and elsewhere in the near neighbourhood. From September to November fourteen more flies were taken by the Veterinary fly boys in the locality.

There was definitely a dry-season infestation of the farm and the flies were certainly subsisting in part on the cattle. They were either resident or filtering up the valley from the main Ntambi river system. Burtt analyses all the captures broadly thus: 35·3% in the shade of the riverine forest, 23·5% in savanna wooding margining the riverine forest, 41·2% in or beside the *Vernonia* thickets. Flies had not been taken here in his wet-season survey. This might have been due (α) to a dry-season spread of hungry flies that infested Tubugwe seasonally only, or (β) to their less ready appearance in the rains.

If the infestations were seasonal the clearings recommended below for the Ngau–Matamondo strip should, Burtt expected, suffice to check the flies.

(ii) *The upper Ntambi river.*

Though the country generally was searched, most of it failed to yield flies. Two were taken in riverine forest, another in *Acacia spirocarpa*-*Disperma* thicket flanking it and one 300 yards away—probably a follower. Further on an extensive richly-grassed woodland of *Isoberlinia–Brachystegia* (miombo) was found near the river near Mulambule with very many zebra frequenting it—but no flies were taken. On the other hand, flies were found commonly in a narrow strip of riverine forest between its crossing by the trade route to Lukando and the confluence of the Ntambi and Mafutu, at which point Baird had taken numbers of flies in August 1930. In spite of the absence of a definite riverine tree element, *G. pallidipes* were captured also near here in the dry river-bed of the Mafutu under conditions of comparative severity. From the junction of the Ntambi and Mafutu onwards evergreen riverine forest began again and the flies became more abundant.

(iii) *The lower Ntambi river and its tributaries.*

The vegetation along the river is evergreen fringing forest; on the lowest eluvial slopes, dry deciduous thicket of *Commiphora-Cordyla*, now largely cleared by settlement. Where the latter has been abandoned secondary dry thicket is regenerating.

Real game is very limited :—a few greater kudu, an occasional bushbuck, the spoor of a single rhinoceros; but bush-pig and baboon are common.

The residual herds of cattle (grazing mainly in the clearings) are watered, generally about midday, at several places along the streams which are situated about half a mile from each other. They then graze in the shade of the trees alongside on the rich grass *Cynodon plectrostachys*, the half-herb *Achyranthes aspera*, and the abundant pods of the large tree *Acacia albida*.

At every cattle watering-place, flies (*G. pallidipes*) were captured by means of the bait-cattle. Flies were taken with less frequency in the riverine forest and on its margins away from the watering-places. Except for two, both evidently "carried," no flies were seen in the settlements or in the dry thicket area.

(iv) *The Matamondo through the Sangwala–Muhoneke–Kikombo area.*

The river from here is dry in the dry season except for four water-holes. The valley is clothed with fine trees of *Acacia albida*, *A. campylacantha*, *A. usambarensis*, and figs, with a good deal of thicket of the trailing *Combretum trichopetalum*, of *Flueggia*, and of *Vernonia senegalensis*. This wooding is from a quarter to half a mile broad and, half a mile below Matamondo, merges into a fine savanna forest of large *Acacia spirocarpa* trees that extends nearly to Godegode. At the point of change to *spirocarpa*, the riverine forest also ceases.

Greater kudu and bushbuck occur, but are rare. There was old spoor of two or three elephants, none of rhinoceros or buffalo. Baboons are extremely common.

G. pallidipes was taken regularly at two of the wells—those of Kihembe and Sangwala—when visited in the morning or between 6 and 6.30 p.m.; the Sangwala well was the most heavily infested. No flies were found there at midday, when the cattle were mostly watered, and the comparatively low rate of loss in the cattle generally of the area is perhaps partly due to the hour of watering. Numbers of the tsetses were taken on the motor road to the Sangwala wells and the flies that are captured at cars and lorries at Matamondo were probably picked up here. At a second well, visited only once, a fly was taken. At a third no flies were taken, but a few were taken in the riverine forest close by.

(v) *Matamondo to Godegode.*

The riverine forest disappears here and tree savanna dominates. Game is much more abundant—with giraffe, a few greater and lesser kudu, and occasional elands. Riverine forest strips occur lower down and in places fringing thickets that seem suitable to the flies. A few *G. pallidipes* were taken on the margins of the wooding as far as Nindi and a female between Nindi and the Nzuhe Lake in very dry thicket, probably following cattle. After this, unaccountably, considering the numbers of game, no flies were seen.

On the Nzuhe and Kimagai Lakes, greater kudu, bushbuck and dikdiks are fairly abundant, as are also rhinoceros that feed on the Euphorbias which they knock down by charging them. But there are still no flies, despite the

proximity of the infested locality at Kidete and the fact that trains pass through constantly from there.

(vi) *Area between Matamondo and Mpapwa.*

Four examples of *G. pallidipes* were captured between Matamondo and Bumira, none between Bumira and Buffalo Creek. But Bumira is only four miles from Kikombo, the Veterinary Station.

TABLE 53.

The apparent preferences of *G. pallidipes* in regard to vegetational communities during the dry season (100 flies captured.)

At watering-places, in river-fringing forest	44·0%
In fringing forest	15·0%
On the margins of fringing forest	24·0%
On car in fringing forest	0·5%
In cultivation on cattle paths	4·0%
On car in dry thicket	0·5%
In dry thicketed ravines	12·0%

Thus, 83·5% of the flies were captured in or beside the fringing forest, while the rest had probably "followed" thence. It would appear that *G. pallidipes* during dry-season conditions in the Mpapwa area is entirely dependent on the shade of the riverine fringing forest. The riverine forest is therefore its dry-season base. Its concentration and feeding-grounds are at the watering-places of cattle, on which probably it is mainly living. See sub-section (iii). The cattle make their contact with the flies at these watering-places.

(e) The situation found by Burtt in the rains.

Burtt reported (1933) :—"During the rainy months the riverine area was observed to be largely choked up with tall grass over eight feet high, the density of which is so thick as to suggest that fly is completely crowded out of the riverine forest. In contrast, the Kidete River, with its open vegetation, was found to be the home of fairly dense fly in the rains. We may therefore assume (i) that *G. pallidipes* is driven out of the fringing forest by unfavourable vegetational conditions during the rainy season; (ii) that the dry-season conditions of the fringing forest, with trampling and destruction of the grass jungle [by cattle], produce a suitable habitat which is annually re-infested by *pallidipes*."

Actually, over-humidity may have contributed heavily to the evacuation of the fringing forest (*see* p. 109 above).

TABLE 54.

The mean hunger stages of the flies (*G. palpalis*) caught near Mpapwa, and the female and young fly percentages, both for the dry season and for the rains.

Season	Mean hunger stage	Female %	Young flies %	Caught on cattle %	Caught on man %	Caught otherwise %
Dry season of 1933	4·0	55·0	15·0	87·0	8·0	5
Rainy season of 1933	3·7	30·3	30·3	60·8	29·7	9·5

(f) Summary.

Burtt agrees that the infections at Tubugwe are of some ten years standing and that there has been little advance in that time. He believes that *G.*

pallidipes was present in August 1930 when Baird failed to find it, but also that it was absent when he himself failed to find it there in the rains. He suggests that the " Ntambi River system is annually evacuated by *G. pallidipes* during the rains and infested again during the dry season, from the east."

While this is fairly probable, I have seen too much of *pallidipes* situations to be impressed by mere failure to find flies.

What is, however, much more impressive than the mere failure to find flies, and lends strong support to Burtt's view, is that in his wet-season survey he could find no flies at all in or beside the fringing forest, even where they were dense in the dry season, but he did take numerous flies under what were then drier conditions, as at scattered, regenerated dry thickets on the watershed. It is doubtful if in the rains he saw so large a proportion of the fly population as he did in the drought, but its distribution was undoubtedly different.

The following points are of special interest :—

1. The fluctuations from year to year in the incidence of trypanosomiasis, on the whole very gradually becoming worse, as in Melsetter in Southern Rhodesia.

2. The relative evacuation by *G. pallidipes* in the wet season of the Ntambi river system which Burtt considers he detected. An annual ebb and flow of *G. pallidipes* is suggested by point 1 above. This varies, but is gradually strengthening in intensity, probably with increasing fly density behind.

3. The dependence of the flies on the riverine wooding in the dry season and their avoidance of it in the wet, when a lighter type of thicket, avoided in the dry season, is used.

4. The scarcity of the flies in the dry season between Matamondo and Godegode despite highly abundant game, riverine wooding (only) having dropped out of the picture.

As regards the practical aspect, the difference between the cases given under Part 2, Section G (*G. pallidipes*) (p. 108 above) and that of Mpapwa is that the country of the sporadic outbreaks in Zululand and Melsetter (in Southern Rhodesia), both of which I know, seems on the whole, except for its river valleys, less suited to the presence of *G. pallidipes* than are Tubugwe and Kikombo. This makes it the stranger that these latter places have not long ago become completely and permanently infested. The danger, however, remains that, with any heavy increase of fly in Ntambi in a favourable season and consequent denser dispersal, Tubugwe and Kikombo may be colonised and the Veterinary Headquarters become untenable.

Burtt recommended the clearing and settlement of portions of the fertile Ntambi–Matamondo–Tubugwe river valleys to check the seasonal spread of the flies. The work done is shown in fig. 23, and its results are discussed on p. 379.

7.—NORTH-WEST HANDENI, TANGA PROVINCE.

In August 1933 Burtt carried out, by request from the Administration, a survey of part of north-west Handeni. Kiberashi, Mgera, Loskitu (Sikitok), Mafisa, Kama, and the country between and around those places were the locality involved.

(a) The situation.

G. morsitans is confined—and will remain confined—to the miombo (*Isoberlinia–Brachystegia* wooding) which here finds its northern and western

limit in eastern Tanganyika. *G. morsitans* is replaced to the north, however, by an uneven infestation of *G. pallidipes*. The following is quoted from Burtt's report:—

North of the road from Mgera to Kiberashi. "The tsetse causing trouble in this area is *G. pallidipes*. According to the natives it has spread in from the Pangani river. . . . It is apparently confined to shady stream-beds during the severe dry-season conditions and later with the flush of leaf in the savanna becomes distributed over wide areas by its own propensity for wandering and possibly by the movements of game.

"Loskitu (Sikitok) Hill. *G. pallidipes* is responsible for the evacuation of Loskitu (Sikitok) hill and its very valuable waters by the Wakwavi. I made a very careful investigation of the area with bait-cattle. . . . The reconnaissance proved that the flies are concentrated in a ridiculously small area of semi-riverine woodland on the west side of Loskitu Mountain (the forest being composed of fairly old trees of *Acacia spirocarpa* thickened up with various evergreen elements belonging to the Vine and Caper families). . . .

"The intervening country between Loskitu and the next *G. pallidipes* concentration, so far as can be judged from a single visit, is approximately 10 miles. Here the flies are concentrated along the narrow length of the Lolderobo–Mafai river, a mere streamlet which, according to Wakwavi and Masai, flows in a northerly direction to the Pangani. It would seem that it is from this rivulet that Loskitu must have become infested with flies moving spontaneously or carried by buffalo and other game, probably during some favourable rainy season, to Loskitu Mountain, where they established themselves, retiring now during each dry season to the particularly suitable area of forest at the foot of the mountain."

(b) Burtt's recommendations.

"It is therefore very desirable that this area of forest be cleared as soon as possible. As it is only just over 400 yards square, a few families of Wanguu (about five) should be settled there. They would have every advantage of fertile soil and adequate water. . . . At the same time a great area of country and very valuable waters would, it is believed, be thrown open to the Wakwavi as a grazing reserve. It is imperative that the clearing of the above area should be done in the dry season . . . in order to exterminate the local fly population which should then die from exposure in the neighbouring unfavourable bush.

"The question of the *G. pallidipes* concentration along the Lolderobo–Mafai rivulet is a difficult problem, as no dry-season water exists along this river and the question of permanent settlement could not be entertained unless a supply could be discovered. However, immediate steps should be taken to clear its course between the villages of Mafai and Mkondo, which lie immediately over the Kiberashi Mountain to the north of it. I took *G. pallidipes* on the Mafai river just below an extremely important watering-place for Wakwavi herds. Moreover, there is a danger of fly being carried over the pass into the Likagura valley near Kiberashi if nothing is done about it. This clearing probably only necessitates the clearing of the valley itself."

Finally stress was laid on the need for keeping clear the valley from Kiberashi to Mgera.

(c) The work done.

The clearing at Loskitu recommended by Burtt has been carried out since, with it is believed complete success.

(d) Points of special interest.

The following points of interest may be noted :—(i) the minuteness of the area of successful infestation at Loskitu, earlier non-existent, but later apparently permanent, which may be compared with the Dar-es-Salaam colony of the same fly, *G. pallidipes* (*see* p. 106 above); (ii) the instance, important in the study of dispersal, which this seems to afford of a successful colony survival (and thereby extension of range) under conditions of carriage or season that were probably temporarily specially favourable, for from this small colony further extension of range might take place during further favourable spells (*see* p. 299 above); (iii) the apparent excellent effect of the discriminative clearing of the one piece of bush, 400 yards square, that was adjudged to be necessary to the flies, bush of other types still remaining; (iv) the fact that in a part of the area investigated *G. pallidipes* appeared to be existing in quantity in very dry country without its usual riverine bases. This may best be illustrated by a full quotation from Burtt :—

" An unusual habitat for *G. pallidipes* was found 20–25 miles north of Mgera during September. Here there is present a dense infestation by this fly of a semi-desert area of approximately nine square miles in the neighbourhood of the small hills Ngabore and Sauni. The country is comparatively flat and is drained by a seasonal water-course that flows northwards towards the Pangani river, but is devoid of riverine fringing vegetation. Frequent sites of Masai cattle bomas showed that large herds of cattle were present about 14 years ago, prior to the invasion by *G. pallidipes*. In the late dry season water is only obtainable from two wells in the river-bed, one at Ngabore, the other at Sauni. Fresh spoor of elephant, rhinoceros, buffalo, lesser kudu, zebra and impala in quantity indicated plentiful game.

" The vegetation of the area [*see* pl. 7, fig. 4] is largely dry thorn-bush with small scattered evergreen thickets, suggesting a habitat for *G. swynnertoni* rather than *G. pallidipes*. The trees are *Acacia mellifera*, *Commiphora Schimperi*, and *Commiphora Scheffleri*, and here and there the general low canopy is overtopped by the flat-topped trees *Acacia spirocarpa* and *Erythrina Burttii*. The small thickets are largely made up of regenerating *Commiphora* with *Grewia villosa*, *Maerua crassifolia* and *Capparis* draped over with the fleshy-leafed evergreen climber *Cissus rotundifolia*. Almost every thicket is surrounded by the succulent Labiate, *Coleus igniarius*, and contains great above-surface tubers of *Adenia globosa* and *Pyrenacantha malvifolia*, both plants sending up their vine-like growth into the general canopy.

" In my opinion these *small, scattered shady thickets* enable *G. pallidipes* to survive the desert conditions of the Ngaborè steppe without the aid of riverine forest.

" The tubers of *Adenia* and *Pyrenacantha* attain the size of a small rhinoceros, which indeed the latter (with their grey wrinkled bark) resemble, and they frequently have holes in them which hive-bees use for their nests. These holes might also harbour the females and pupae of the tsetse. On the other hand, the flies must have been experiencing distress—for while we were passing through the above-mentioned country in the heat of noon on September 29th, my party and I were attacked by *G. pallidipes* in considerable numbers and were bitten continuously behind the knees and on the ankles. The flies caused an audible ' buzzing ' sound through sheer numbers. All those caught proved to be hungry males—an observation for *G. pallidipes* that is contrary to all our previous experience with this fly in Tanganyika. Normally the flies

become active in the cool of dawn and in the late afternoon and females preponderate" (Burtt).

8.—THE GENERAL PROBLEM AT HANDENI, TANGA PROVINCE.

(a) The economic situation.

Handeni (6,000–8,000 square miles) is divided roughly into three sections—the former rain-forest area of the south-west with high rainfall and very rich soil; the fair-rainfall, fair-soil area of the entire east; and the dry country of the north-west, practically uninhabited north of Mgera, dealt with above.

The district is occupied by two tribes, the Wazigua in the east and the Wanguu in the west; their population totals something upwards of 60,000 with a density of from 7 to 10 persons to the square mile, and with seldom more than ten families together. One hundredth or less of the district is under cultivation, the rest being bush.

The Wazigua in particular are liable to recurrent famines. Their country, though inferior to the abnormally rich country of the Wanguu, is by no means lacking in fertility, nor is it inferior to many large parts of the Tanganyika Territory in which no famine occurs. The rainfall, even at Handeni, regarded as specially dry, is 32 inches, while 50–60 inches fall in Nguu. But the water-supply is defective in Uzigua. The people are pleasant but abnormally thriftless and unenterprising. With pastoral traditions, they cultivate the smallest patches on which they can possibly subsist with a miserable type of miniature, misshaped hoe, with which proper cultivation is impossible. Through a belief that the eating of cassava causes abortion, they have steadily resisted its planting as a food reserve, though urged to do so by every District Officer both under the Germans and ourselves. Despite all this they normally raise sufficient to live on. But when, once in every six or seven years, a mal-distribution of rainfall occurs, their sins are inevitably punished.

Early in 1934, after the relief of the latest famine had cost the Government much money, the proposal came up that they should be transplanted into the large unoccupied portions of the very rich country that belongs to their neighbours the Wanguu. A large part of the district is under tsetse infestation, light or heavy, and it was felt that the opportunity might be a good one for bringing about concentrated settlement and so guarding against the effects of any future incursion of sleeping sickness. Thus two objects might be obtained by this step.

A meeting to discuss the proposal was held at Handeni on 25th June, 1934, on the instruction of the Chief Secretary. There were present the Provincial Commissioner, Tanga (Mr. C. H. Grierson), the Sleeping Sickness Officer (Dr. G. Maclean, O.B.E.), the Assistant Conservator of Forests, Lushoto (Mr. W. F. Baldock), the District Agricultural Officer, Tanga (Mr. J. C. Eyre), the District Officer, Handeni (Mr. S. B. Jones) and myself. Points of interest at the meeting were:—

(i) Dr. Maclean's statement that, in light of past experience, an average African family needs not less than sixteen acres for its normal requirements. The total population of Handeni district could be concentrated in 300 square miles.

(ii) his view that, if tsetse infestation were general and sleeping sickness were to arrive the people would have to be concentrated in settlements with a minimum of 1,000 families apiece.

(iii) the District Officer's view that increased cultivation would solve the

problem without concentration, and the Agricultural Officer's objection to this that owing to the scattered population it would take four permanent agricultural assistants to effect increased cultivation.

(iv) the Provincial Commissioner's suggestion of a solution by means of an organised storage of grain for lean years, on the lines of the biblical precedent.

(v) the suggestion that the population of 2,000 families of the Mazingara chiefdom should, as a preliminary and exploratory step, be moved into the rich Kimbe chiefdom of Uzigua, occupied by only 1,400 tax-payers, and that the surveys necessary for this should be made. These were to include an agricultural survey by the Agricultural Officer and a survey of vegetation and tsetse by the Tsetse Research Department.

(vi) the view strongly emphasised by myself that there should be borne in mind, in concentrating settlement or freeing areas locally of fly, the object of creating a tsetse-free and settled corridor of country on or parallel with the main Kilosa–Korogwe road, as a continuation of the heavily settled strip already existing from Kilosa to Turiani and the neighbourhood of Kanga Mountain.

(b) The survey work done.

Some parts of the district and their former fly situations were already known to me from brief visits at previous periods, while the north-western part, as stated above, had been surveyed by Burtt. After a preliminary reconnaissance on which I was accompanied by Mr. Eyre, I launched Swedi, our head fly boy, with assistants, on a general survey. This was still incomplete at the end of the six weeks allotted and will be concluded later. The general position meantime, as regards tsetse, is given below.

(c) The vegetation of the district.

The vegetation of Uzigua may be summarised as follows :—a broad band of miombo stretches across the south of Uzigua and, extending on to Unguu, forms the northernmost continuous section of the great *Isoberlinia–Brachystegia* belt, which narrower or broader, broken or solid, runs up through the eastern third of Tanganyika from far south of the Rovuma. One arm runs north past Mgera, another passes between Uzigua and Pangani, and separated patches occur in the north of Uzigua, as at Sindeni.

It is important in relation to tsetse to note that the rest of Uzigua, largely on red soil and constituting a large part of the area, is dominated mainly as regards slope (eluvial) vegetation by *Combretum splendens* and *Zeyheri* and *Ostryoderris stuhlmannii*, with their usual associates including, here, much *Acacia pallens* ; as regards drainage line vegetation by *Acacia campylacantha* and its associates. Where the country is unburned, closed forest persists or regenerates, often consisting of the valuable *Brachylaena Hutchinsii* and its tree and dense evergreen-shrub associates. A transition between this and true rain forest is present as well.

The vegetation of Unguu is as follows :—zones of immensely rich soil flank the mountains in Unguu. These are the areas most recently stripped of rain forest and carry a rank, tall grass-growth, bound together with leguminous climbers, such as *Canavalia* and *Mucuna*. A crest of rain forest persists on the ridges of the mountains and patches survive in the valleys. Immediately outside these zones, as a further stage in a deteriorating succession caused by fires, begins the miombo woodland of high *Brachystegia* trees on soil that for miombo is splendidly rich and that carries a close and more or less high growth

of grass. This covers the lower hills. Rich valleys characterised by *Acacia campylacantha* split these rises apart or run up the sides of the latter as shallow depressions with open bush of *Combretum ternifolium* and groves of stink-bark (*Acacia usambarensis*) and one or two other species.

(d) The tsetse flies of the district.

The miombo (*Isoberlinia–Brachystegia*) areas are infested generally with *G. morsitans*, and their northernmost points are the northernmost points of the occurrence of this fly in the eastern strip of east Africa. I also obtained an example of *G. austeni* at Kilwa in Nguu.

The *Ostryoderris–Combretum–Acacia pallens* areas are usually nearly devoid of *G. morsitans*. Stragglers of the species enter them and an occasional example of *G. pallidipes* has been taken, while I took one *G. brevipalpis* in this type of country a little south of Handeni in January 1920. Further, from my observations in the past I judge that a light infestation of parts of this vegetational community takes place on the part of *G. morsitans* from the miombo in particular years or year-cycles, but that the general situation to-day is by no means worse than it was when I saw it in 1920 and again in 1926.

Briefly, the Uzigua country is relatively free from tsetse. It offers large and frequent fly-free spaces, and cattle are kept here and there. The Unguu country is more heavily and generally infested. The survey has yet to be finished, but it is already apparent that a general movement of population from Uzigua into Unguu would be a movement from a very lightly and patchily infested area into one more strongly and permanently infested.

It is specially, therefore, from the motive of famine-prevention that such a move might take place. It is interesting from this point of view to note what are the possibilities of reclaiming fly country in Unguu.

(e) The possibilities of expelling *G. morsitans* from infested parts of Uzigua with the aid of, or in conjunction with, settlement.

The district as a whole is well-grassed, the miombo (*morsitans*) country being unusually well-grassed for this type of wooding. Parts of it also carry little thicket and could probably be attacked successfully by our method of late, organised, grass burning. Better still, and applicable to the rest of the area as well, would be abstaining from burning altogether. From the agricultural view-point a stoppage of burning to as great an extent as may be possible would be a great boon. There are plenty of indications that this country would be specially responsive, that valuable closed forest would extend, and that improvement of the soil would ensue. Improvement of the waters would probably follow the expansion of the forest. A small forest reserve in Uzigua had thickened up wonderfully through protection from fire, and the sight was to be seen of *Combretum Zeyheri* and other trees of the savanna being hustled and choked by the plateau-forest elements of the area and invaded by the useful tree *Brachylaena Hutchinsii*.

But *G. pallidipes* is sparsely present here and there, and we have not yet proved what the effect will be on an infestation of this tsetse of keeping the grass unburned and thus encouraging thicket. Experiments in this connection are planned when Moggridge's investigation of this species at Kilifi is finished. Such experiments might take place in Handeni.

In Unguu control might be brought about in other ways. If the Wazigua are moved into Unguu, or the Wanguu themselves are concentrated, there should on no account be a solid concentration. The valleys that have been

referred to as splitting the miombo resemble part of an arterial chart and carry some of the richest soil in Tanganyika. These only should be broadly settled, together with the *Combretum*-characterised depressions that form their shorter tributaries. This would result in the isolation of the miombo-covered rises between and, I feel sure, in the disappearance from them of *G. morsitans*, deprived of its feeding-grounds in a country in which game is not plentiful and which is still suffering, as regards numbers, from the effects of the great rain of 1929–30. This disappearance would be particularly likely if the grass were kept unburned for a few years in succession, but the position in regard to *G. pallidipes* would need to be carefully considered. The one other objection to not burning is that the natives now burn for the protection of their gardens from bush-pigs. This in any case does not protect them in the long-grass season when the crops are ripening and vulnerable, and a close community would be able to deal with this menace far better than the present scattered villages. With the effect on the fly that is expected to be attained the general result should be a network of close population with large and richly-pastured cattle-grazing areas between.

(f) Points of special interest.

The first point of special interest lies in the confirmation from the traverse made by myself from Kilosa to Handeni, and my reconnaissance and Swedi's survey in the latter district, of the fact that in the greater part of this very extensive *morsitans* fly belt the grass-growth is unusually excellent and the "D.P." (densification potential) good—were fires excluded. It is the obvious measure to apply here if once the doubt regarding *G. pallidipes* were satisfactorily settled.

Secondly there is the statement obtained from the natives generally that in Unguu there was a tremendous drop in the numbers of the flies (*G. morsitans*) following heavy downpours in the 1929–30 season, when this species was decimated at Kikore. In Unguu it is not low-lying flats that are concerned, as at Kikore, but a damp, rank-grass, high rainfall area, and the effect might well have been the same. Even now the flies have not recovered. In the past much fluctuation of density and distribution of tsetse has been known to occur in this district, and it may have been due to such causes.

Finally there is the strong suggestion that the flies might be expelled by settlement of the rich river-valleys only.

9.—MKWAJA, PANGANI DISTRICT, TANGA PROVINCE.

At the request of the Administration Moggridge was deputed to conduct a survey of the fly situation at Mkwaja, on the coast south of Pangani.

The first herd of 50 head of cattle was introduced in German times from Uzigua in Handeni. The number had risen to 400 by 1929, when they began to die off and their grazing area was changed, though they had still to use the old waters. In 1934 there were 154 head and about 90 small-stock, and of the cattle five were obviously fly-struck. Recommendations were wanted.

A strip of intensive cultivation, heavily planted with mango trees, between 400 yards and 800 yards wide, follows the ridge of high ground along which the main coast road runs, from Maliamu nearly to the Mkwaja river, and a belt of coconut palms, 200 yards broad, fringes the coast and extends off along it to north and to south. Otherwise the dominant communities, away from the immediate influence of the rivers, are of the slender gall-acacia, *A. seyal*, and, west of the road especially, of the palm *Hyphaene coriacea*, occurring in

special density south of the Mkwaja river. Small belts of *Combretum–Terminalia* wooding intrude. Three streams cross this sandwich-like belt—the Mafuni, Mkwaja, and Maliamu. The lower course of the Mafuni is much and widely thicketed. The vegetation of the upper reaches of the Mkwaja is purely marginal and mostly light, but 800 yards below the road the river makes an "S" bend and the marginal vegetation thickens considerably. Two hundred yards lower still are the two water-holes used for watering cattle. These were found to be the main source of the trouble.

Monkeys (*Cercopithecus aethiops*) and baboons (prob. *Papio cynocephalus*) are common in the vicinity of the rivers and crocodiles are present in the lower reaches of the Mkwaja. Two reedbuck were seen and the wet-season footprints of giraffe. Otherwise game appeared to be absent. It is always, the natives said, very scarce.

A light infestation of *G. pallidipes* was found along the Mkwaja and in the general bush, scrub and thicket. One example of *G. austeni* was taken. *G. pallidipes* was taken in the thickets of the Mafuni also, but not on the Maliamu or on the high ground from which all these small streams originate. A slightly heavier and wider distribution of the flies is to be expected in the rains.

As soon as Moggridge located flies on the Mkwaja he suggested the use of oil drums, at which the cattle might be watered from one of the wells in the village. The Assistant District Officer, Capt. Collingwood, provided these and the cattle were thus watered. This is a temporary measure only.

The real measure recommended was the reclamation of the water-holes by cutting out the vegetation along the Mkwaja from the main Dar-es-Salaam road to a point 1,200 yards further down: this vegetation is very narrow and for over half the distance very light. Certain thickets and scrub should go also, the object of the clearing being to prevent the passage down-river of the fly from west of the road. Herdsmen would still have to be warned to keep their cattle away from the edges of thick bush and scrub and from riverine thicket. It was estimated that 1,200 men-days should suffice for the task. The purchase of axes would be necessary.

At present the grazing is remote from the village of Mkwaja. This could be remedied and a small amount of clearing on the upper reaches of the Mafuni should release a great area for grazing. The clearing of a strip of thickets about 1,000 yards long by 500 yards wide should suffice.

The following points are of special interest:—

(i) the by no means unusual situation in which *G. pallidipes* is found infesting country in the almost complete absence of game;

(ii) the fact that this case is typical of the instances, in Uganda and Tanganyika, in which the infestation by tsetse of water-holes only prevents use of country or causes losses in the stock using it. As soon as the water is freed, mortality ceases or the country becomes capable of being grazed, provided that the herding is intelligent; and

(iii) the recommendation of what amounts to discriminative clearing only, such as appears to have been effective against the same fly in Mpapwa and on the border of Melsetter in Southern Rhodesia.

10.—RECONNAISSANCES AND SURVEYS FOR THE SELECTION OF A STATION FOR EXPERIMENTAL ATTACK ON *G. MORSITANS*.

(a) Tabora–Nzega–South Kahama.

This was carried out in 1934–35 by Jackson. "The object of the preliminary surveys (1934) was to select sites for experimental attack on *G. morsitans* and

to choose a centre for research to start in 1935 and to be continued over several years.

"It should be explained that according to the classical investigations of Jack (1911, 1912), Shircore (1914), and Swynnerton (1921), *G. morsitans* becomes concentrated in the dry season about drainages where trees are less deciduous owing to subsoil moisture and whither game animals are attracted at such times by water or young grazing. The Department's researches on *G. morsitans* in the Central Province of Tanganyika failed to confirm these findings, but it was always realised that the country studied there was not very typical of the huge areas infested by this tsetse in other parts of Tanganyika, in the Rhodesias, in Portuguese East Africa and in our Western Province. For this reason it was always the intention to prosecute subsequent researches in the great western fly belt of the Territory.

"Topography. The country explored in Tabora, Nzega, and Kahama districts in 1934 is covered with miombo woodland on all the eluvial soils, whether on hills or the scarcely-perceptible rises of vast plateaux. The country is traversed by two large rivers, the Igombe in the centre and the Ugala in the south, and their tributary streams. Both flow westward, the Igombe emptying into the Malagarasi swamp and the Ugala into the Malagarasi River near its mouth, in Lake Tanganyika.

"The vegetation of the eluvial soils. The miombo wooding on eluvial soils is more or less thickened by the shrubs *Phyllanthus discoideus* and *Abrus Schimperi*, the second mainly in the north. *Isoberlinia globiflora* is the dominant large tree; the allied genus *Brachystegia* is represented by at least eight species variously distributed, some of which are apparently found only in this area. Important smaller trees include *Combretum Fischeri*, *Commiphora Fischeri*, *Strychnos pungens*, and *Diplorhynchus mossambicensis*.

"The vegetation of the interzones. In many parts the miombo is separated from the alluvial soils by a band of *Acacia rovumae*, with *Lannea humilis* and an associated flora which sometimes includes groves of *Acacia Fischeri*. *Terminalia sericea* may be common.

"The vegetation of the lighter alluvium. In the broad drainages leading to the big rivers there is but little of the heavy alluvial 'black-cotton' soil so characteristic of other parts of east Africa. The common type of mbuga is a light alluvial soil covered more or less uniformly with a sandy wash from abundant large ant heaps. The dominant large tree is the hard-wood *Afrormosia angolensis*. Common smaller trees are *Crossopteryx febrifuga* and *Combretum ternifolium*. The ant heaps are covered with thickets of *Canthium* and *Grewia* and crowned with *Mimusops densiflora*, *Diospyros*, and other large trees.

"The vegetation of the heavier alluvium. Where 'black-cotton soils' occur, the dominant large tree is *Terminalia torulosa*, while of smaller trees *Combretum ternifolium* and one or other of the gall-acacias abound—*A. formicarum* in the north, *A. Burttii* in Kahama and locally elsewhere, and *A.* sp. nov. in the south.

"The vegetation of the rivers. The rivers and their larger tributaries are dominated by *Sizygium guineense* with thickets of *Canthium*, among which stand *Diospyros* and other large trees. Of the lower vegetation, *Aeschynomene*, *Acacia orfota*, and *Sesbania aegyptiaca* are common.

"The fauna. The characteristic large mammals of the great miombo are the sable antelope, Lichtenstein's hartebeest, the southern reedbuck (*Redunca arundinum*) and the oribi. Animals very common in the great

miombo as well as in other areas include roan antelope and common duiker, and, on the alluvium dominated by *Afrormosia angolensis*, topi. Other species more or less common are giraffe, zebra, and eland generally; greater kudu and klipspringer in hilly parts; waterbuck, bushbuck, hippopotamus and crocodile in and about the big rivers; and, amongst smaller game, impala, steinbuck, wart-hog, bush-pig and baboons are widespread. Dikdik are less common than in some other parts of the Territory. Elephant and buffalo are migratory or local; rhinoceros are not found in the Great Miombo proper, though abundant in the drier miombo of the Central Province.

"Distribution of the tsetse. To the north-east of Kakoma, and about 25 miles away, begins a more hilly stretch of almost uninhabited country in which *G. morsitans* presents a remarkably uneven distribution, except that it is uniformly dense along a drainage (Nyahua) bounding the area on the east. Elsewhere flies are found commonly in half-a-dozen or fewer concentrations, against which it should be interesting to experiment in attack. Throughout Kahama, Nzega, and Tabora generally the density of *G. morsitans* is most uneven. Thus, about Kahama itself, 'fly' is much commoner at and south of that place, and much scarcer to the north. The reasons for this and for similar unevenness of density elsewhere are not obvious and call strongly for intensive research.

"Choice of station. In all respects, vegetationally and faunistically, the country southward from Tabora was most in accordance with the description just given, and has been selected as the area for the contemplated research and experimental attack on *G. morsitans*. A research centre was chosen at Kakoma, a water-hole situated some 65 miles south of Tabora, in an uninhabited tract of country some 100 miles across. Undisturbed conditions were assured by the earlier removal, due to epidemic sleeping sickness, of all natives who formerly lived in those parts. The country is flat and featureless, thus providing large stretches of homogeneous vegetation types suitable for research.

"Sites for Field Experiments. A large area of about 400 square miles between Kakoma and the Ugala River has been earmarked for an experiment in prohibition of grass burning. It is intended to use Kakoma itself as a control, and to prohibit fire in half the experimental area from 1936, and in the remaining half from 1937. In this way half the experiment will always be one year ahead of the other half, and by comparing the two halves with each other and with the control we should learn much about the detailed effect of the measure, whether it be successful or not.

"In the hilly country to the north-east of Kakoma referred to under 'Distribution of the Tsetse' the intention is to try the effect on the tsetse-concentrations of progressive experiments in discriminative clearing, and perhaps of measures involving exclusion of game animals.

"Experimental plantings of possibly useful trees and shrubs for densifying the woodland, by natural spread under conditions of non-burning, have been begun.

"Meanwhile intensive studies at Kakoma are in full swing, and include determination of true density of both sexes, causes of activity (willingness to appear to man), study of rates of larviposition, emergence, death, and dispersal, physiological condition, concentration habits, and effects of different densities of game animals on the tsetse. Longer range work has been begun on the causes of uneven distribution referred to above, and in addition certain incidental studies are mainly directed to answering criticisms of methods past and present." (Jackson.)

(b) North Kahama, Biharamulo, North Kilosa.

As these areas have not been selected for immediate work, it is sufficient here to say that it is clear from my reconnaissances that the D.P. (densification power) almost throughout them is, for miombo, excellent. Thus, if our non-burning method proves useful, we have in Tanganyika Territory very great areas indeed to which it will certainly be applicable if *G. pallidipes*, *G. brevipalpis*, and *G. austeni*, where these are present, do not prove capable of defeating it.

11.—RECONNAISSANCES CARRIED OUT IN TANGANYIKA WITH THE OBJECT OF FINDING A DENSE INFESTATION BY *G. PALLIDIPES* AS A SUBJECT FOR STUDY.

(a) Nindo, western Shinyanga.

In 1923 I found what appeared to be a heavy infestation of *G. pallidipes* in Nindo, in country illustrated in pl. 5, fig. 3. Moggridge was sent there in July of 1934.

The country may be divided "into two main groups—great mbuga systems occupying all low-lying land and heavily wooded areas on higher ground. The great stretches of mbuga are devoid of trees but many of the smaller mbugas support *Acacia*, *Combretum* and other genera. The higher ground supports many species of trees and shrubs, for the most part closely growing and showing a tendency to form individual thickets" (Moggridge, report). The wooding is typical of much *swynnertoni* country, described in Part 2, Section F (pp. 86 and 87 above). *Strychnos heterodoxa*, *Commiphora ugogensis*, *Commiphora Fischeri* and *Ostryoderris Stuhlmannii* with much thicket of *Abrus Schimperi*, *Markhamia obtusifolia*, etc. on the drained ground (*see* pl. 5, fig. 3); elsewhere *Lannea humilis*, *Commiphora Schimperi* and their associates. "During the reconnaissance it was noticed that the more heavily thicketed areas were the least productive of *G. pallidipes*. The greatest density was found on a section of the old German road which passes through the settlement of Nindo. This area of *pallidipes* is five miles from Nindo (west end) on what would appear to be the highest point on the road. The soil of this section, which is perhaps one mile in length, is red eluvial. The bush, dry and leafless at this time of year, is thicketed, but not densely, and is characterised by many large trees. Other than at the place just described the flies were too scanty to be worth mentioning.

"As regards the game of these parts at this time of year it may be said that it is almost entirely absent. Two ostriches and three small buck were seen but that was all. Game birds were unusually common, large numbers of guinea-fowl were constantly met with and francolin and sandgrouse were also very common" (Moggridge, report, 5.viii.34).

There are two points of special interest: First there is the apparent reduction in the numbers of *G. pallidipes* between the dry season of 1923 and that of 1934, though general infestation was still present. It is impossible to account for this, probably a mere fluctuation, with the history in between unknown. *G. swynnertoni* was present in great density. Secondly there is the absence of mammalian game, though the game birds are abundant. The opportunity would have been a good one, if it had been foreseen, for an examination of the gut-contents of the numerous *G. swynnertoni* to ascertain if they were feeding on the birds.

(b) The Rau Forest, south of Moshi.

A brief reconnaissance of the Rau rain forest, south of Moshi, was undertaken on 5th and 8th October, 1934. On the former date the forest proper was entered and much heavy timber and planted rubber encountered. On the latter occasion the fringe of the forest on the north-east side was worked. The time available was too short to permit of a thorough investigation, but both *G. pallidipes* and *G. brevipalpis* were present in the forest and on the outer fringe. A summary of the flies is given below :—

Heavy forest	9.40 a.m. to 11.37 a.m.	*G. pallidipes* 5 : *G. brevipalpis* 4.
,, ,,	4.30 p.m. to 5.50 p.m.	*G. pallidipes* 6 : *G. brevipalpis* 17.
Forest fringe	10.25 a.m. to 11.45 a.m.	*G. pallidipes* 4 : *G. brevipalpis* 0.
,, ,,	4.25 p.m. to 6.03 p.m.	*G. pallidipes* 9 : *G. brevipalpis* 1.

G. pallidipes was found to be spread right through the forest (in which lumbering has for many years taken place) and Moggridge believed that a fuller survey would disclose patches of high concentration.

(c) Pare.

Between the Tanga–Moshi railway and the Pare Mountains, at Kiswani, and at streams crossing the road, Moggridge's fly boys took three *G. pallidipes* in several hours' catching. In January 1920 I took this fly in greatest numbers in the " rhino " thicket of succulents—*Euphorbia* spp., *Sanseveria*, Crassulaceae, etc., just west of the railway (pl. 5, fig. 4).

(d) The Tongwe–Kiwanda area, east Usambara.

" The area round the Y.M.C.A. Mission at Kiwanda was worked and so, to a lesser extent, was the area round about Tongwe. *G. brevipalpis* was encountered in numbers everywhere, but *G. pallidipes*, although generally met with, was found in small numbers only." The results of the puparia searches have been given under *G. austeni*; large numbers of the puparia of the last-named fly were found. " It is amazing that no *brevipalpis* pupae or cases have been found although the fly is common and representative sites have been searched."

Pigs were fairly common but nocturnal. Monkeys were present but not numerous. Crocodiles and monitor lizards were present in the rivers. These and a grey duck were watched for long through glasses but no flies came to them.

The following points are of special interest. In the first place there are the further instances (at Kiwanda and Pare) of the small numbers in which *G. pallidipes* can survive and effectively occupy country. It is true that the centres of the infestation may not have been discovered. Secondly there is the fact that with only (so far as could be found) one effective food animal present and that one nocturnal, a light population of *G. pallidipes*, a heavier one of *G. austeni*, and a heavy one of *G. brevipalpis*, were able to maintain their existence. That the first and last of these flies are able to find sleeping bush-pigs in at any rate very high grass has, however, been shown by myself in Mossurise (Swynnerton, 1921 : 337).

I am much indebted to Canon Hellier for his loan of a house to Moggridge and for his general kind assistance; and, for similar help, to the Director of the Amani Institute.

This series of reconnaissances was extended into Kenya Colony and further details are given in Part 8 (*see* p. 449 below).

PART 6.—RECLAMATION AND SETTLEMENT, WATER SUPPLY, AND SOME RECLAMATION TECHNIQUES.

A.—THE CLEARINGS MADE IN THE PERIOD 1931–34.

1.—SHINYANGA.

The scheme which I first laid down in 1923–24 has been continued and much developed. Both tribal labour and labour paid for from the funds of the Tsetse Research Department have been employed, the latter where the experimental aspect appeared at the time to preponderate. Actually, however, two-thirds of the clearings made in the past four years from our funds are already settled with natives. Further we have had to contribute heavily to the cost of the tribal labour in order to enable it to carry on at all with its side of this co-operative work in the recent years of financial difficulty.

The native authorities in Shinyanga have spent in four years some £156, while the Department has expended £995 on tribal labour and £2,715 altogether on work beneficial to the tribe. These figures do not include the salaries of those members of our permanent European staff who have devoted much of their time to the surveys, supervision, and other work that has led to the reclamation.

TABLE 55.

Contribution to reclamation in Shinyanga by the Tsetse Research Department and by the Native Treasuries.

Year	Contribution by Native Authorities £	Contribution by Department £	Indirect contribution by Department £
1931 . .	10	20	305
1932 . .	36	150	1,320
1933 . .	55	315	40
1934 . .	55	510	55
Total . .	156	995	1,720

In every case (tribal and other) in Shinyanga, the site of the clearing has been selected and its outlines marked out by ourselves, the supervision of the workers has been carried out wholly by our European staff and trained native assistants, with such tribal heads as attended, and the clearings have been carried out by methods of our selection. We have recruited our own labour for the paid clearings. The Administration has dealt with the Chiefs, and, through them, the natives, and secured the attendance of the latter at tribal clearings. The co-operation and the spirit of all has been perfect, and it is only by such co-operation combined with a single expert control or guidance of the actual operations that each instalment of work can be fitted into a large general scheme such as this is without wastage and, often, bad clearing.

2.—KWIMBA, MASWA, MWANZA, MUSOMA, NZEGA, KAHAMA, MBULU, AND KONDOA.

Renewal of our work in aid of the Administration and tribes in these districts took place from 1932 onward.

TABLE 56.

Clearings effected by, or under the supervision of, the Tsetse Research Department, in various districts during the period 1931–34.

Year	Name of clearing	Purpose	Nature of clearing	Method employed	Labour	Size	Settled or not	Labour in man-days	Contribution by the Tribe	Contribution by the Department *	Total
									Shs.	Shs.	Shs.
			1. *In the Lake Province.*								
			(*a*) In Shinyanga District.								
1931	Broadening and cleaning old clearing, east side of Block 3.	Isolation of Blocks 4A and 4B.	B xx, Part O.C.†	Permanent.	Paid.	1·6 miles × 400 yds.	Settled.				
	Cleaning of game fence clearing.	Separation of Block 11 from Block 5A.	A x, Part O.C.	Temporary.	Paid.	4·4 miles × 800 yds.	S.				
	Cleaning of the Ningwha river clearing.	Isolation of Blocks 4A and 4B.	G xx, Part O.C.	P.	Paid.	1·2 miles × 900 yds.	S.			6,080/93	6,080/93
	Shinyanga Rocks clearing.	do. do.	C xx.	P.	Paid.	2·3 miles × 1000 yds.	S.				
	Ndama river clearing.	Separation of Blocks 5A and 5B.	A x.	P.	Tribal.	2·4 miles × 800 yds.	S.	11,780			
	Plots clearing.	Separation of Blocks 4A and 11.	½ C xx, ½ G xx.	P.	Tribal.	1·3 miles × 500 yds.	S.	4,000	200/00	413/88	613/88
1932	Seke Road clearing.	Isolation of Trapping Block.	D x, Part O.C.	P.	Paid.	1·7 miles × 1000 yds.	Part S.				
	Ngongho river clearing.	do. do.	G xxx.	P.	Paid.	2·7 miles × 400 yds.					
	Mwamala clearing.	do. do.	G xx.	P.	Paid.	3·35 miles × 1000 yds.					
	Cleaning of Seseku clearing.	Separation of Block 7A from 7B.	C x, Part O.C.	P.	Paid.	5·34 miles × 1000 yds.	S.				
	Manyara clearing.	Separation of Block 7A from 7C.	C xx.	Semi-P.	Paid.	3·0 miles × 1000 yds.	S.				
	Cleaning and piling of portions of Ningwha river, Block 3, "Plots" and Shinyanga Rocks clearings.	Isolation of Blocks 4A and 4B.	Described above under two separate clearings.		Paid.	Refer to 1931 programme.	See above.				
	Mantine Hills clearing (2nd portion).	Isolation of "Outer Circle."	C xxx.	T.	Paid.	4·6 miles × 1000 yds.	S.			26,401/39	26,401/39
	Thicket clearing in Block 5A.	Reclamation of Block 5A.	G xxx.	Semi-P.	Paid.	Over an area of 10·5 sq. miles.	S.				
	Thicket clearing in Block 5B and part of Block 11B.	Experimental reclamation measure.	G xxx.	Semi-P.	Paid.	Over an area of 16 sq. miles.					
	Thicket clearing on Ningwha stream.	Reclamation of the "Outer Circle."	G xxx.	Semi-P.	Paid.	3·75 miles × 400 yds. (approx.).	S.				
	Clearing of Triangular Thicket "Outer Circle."	do. do.	D xxx.	Semi-P.	Paid.	¼ sq. mile.	S.				
	Chibe clearing.	Isolation of "Inner Circle."	C xx.	Semi-P.	Tribal.	3·7 miles × 400 yds.	S.	7,600			
	Mwantine Hills (1st portion).	Isolation of "Outer Circle."	¾ C xxx and ¼ G xxx.	Semi-P.	Tribal.	1·4 miles × 1000 yds.	S.	2,796			
	Beda Road clearing.	Cattle Corridor to Huruhuru.	C xx, Part O.C	P.	Tribal.	7·2 miles × 1200 yds.	Part S.	35,604	723/00	3,025/73	3,748/73
	Beda Road Extension clearing.	do. do.	do.	P.	Tribal.	3 miles × 1400 yds.	S.				
	Mhumbo river clearing.	Freeing of Mhumbo river from fly.	F x, Part O.C.	P.	Tribal.	2·8 miles × 800 yds.	S.	8,421			

† See explanation below.

* Excluding European staff.

1933	Clearing of Ndama river (tax defaulter labour).	Experimental reclamation of Block 5 B.	G xx.	P.	Paid.	3·0 miles × 200 yds. (approx.).	Part S.			791/29	791/29
	Clearing of hard-pan thickets in Block 5A.	Reclamation of Block 5A.	C x.	Semi-P.	Paid.	Over an area of 10½ sq. miles.	S.				
	Clearing of hard-pan in "Outer Circle."	Reclamation of "Outer Circle."	C x.	Semi-P.	Paid.	Over 5 sq. miles.	S.				
	Cleaning of Ushola clearing.	Making safe entry to Beda Cattle Corridor.	C xx, Part O.C.	P.	Tribal.	6 miles × 1000 yds.	S.	6,810	1,100/00 for 1933.	6,338/69 for 1933.	7,438/69
	Separation of ilula bush from main bush from Stiebel's Tank to Half Way Camp to the west, and from Stiebel's Tank to the Seke Road to the north.	Reclamation of the Huruhuru gall-acacia wooding by isolating it from the true habitat of the fly.	H xx.	P.	Tribal.	18 miles with a minimum breadth of 1200 yds. Many open stretches.	S.	22,520			
	Clearing of all but gall-acacia bush from Sayu.	Destruction of this stepping-stone to infestation of the above.	C xxx.	Semi-P.	Tribal.	4 sq. miles.	S.				
	East Block 9 clearing.	Making the Mhumbo river safe for cattle.	C xx, Part O.C.	Semi-P.	Tribal.	2 sq. miles approx.	S.	8,820			
	Mwantine Break-through.	Cattle Corridor to Huruhuru from the south.	C xx, Part O.C.	Semi-P.	Tribal.	3·2 miles × 2 miles.	S.	9,120			
	Ngongho Pools clearing.	To make them safe for cattle to water.	C xxx.	Semi-P.	Tribal.	Approx. ¼ sq. mile.	S.	4,000			
	Mhumbo river and cleaning up of Block 7C, mbuga system.	To make river safe for cattle and to open new mbugas for grazing.	F x, Part O.C.	Semi-P.	Tribal.	11 sq. miles approx. (much light clearing).	S.	10,530			
	Block 6 Triangle clearing.	Destruction of bush promontory at south of Blocks 5B and 11B.	D xx.	Semi-P.	Tribal.	1 sq. mile approx.	S.	5,230			
	Kisapu clearing.	Destruction of island of fly.	C xx.	T.	Tribal.	Incomplete.	S.	17,700			
	Ilola clearing.	To give a hard and fast line to the south edge of Nindo Bush.	H xxx, Part O.C.	Semi-P.	Tribal.	2·5 miles × 800 yds. (approx.).	S.	9,500			
	Half Way Camp Tank.	Water for the Huruhuru.			Tribal.	Small trial tank.		280			
	Sayu Tank.	do. do.			Tribal.	Capacity 700,000 gallons.		3,400			
	Miscellaneous.	Grass cutting, etc.			Tribal.			4,000			
1934	Clearing of remaining bush (excepting big trees) on the hard-pan strips in Block 5A (pl. 13, fig. 1).	Reclamation of Block 5A.	C x.	Semi-P.	Paid.	Over an area of 10½ sq. miles but not completed.	S.			1,068/98	1,068/98
	Clearing of Butuyu.	Destruction of a source of infestation of the Huruhuru.	C xx.	Semi-P.	Tribal.	1½ sq. miles approx.	S.	17,730			
	Broadening of clearing separating gall-acacia bush from the main bush from Stiebel's Tank to Seke Road.	Reclamation of the Huruhuru areas by isolating them from the home of the fly.	H xx.	P.	Tribal.	13 miles with the minimum breadth of 1933 clearing extended from 1200 yds. to 1 mile.	S.				
	Broadening of Beda Road Extension clearing.	Increasing margin of safety in Cattle Corridor.	C xx.	Semi-P.	Tribal.	1¾ miles × 500 yds.	S.				
	Clearing of remaining bush on Sayu.	Making this bush "island" quite safe for cattle.	H x.	P.	Tribal.	4 sq. miles.	S.				
	Mwantine Break-through.	Continuation of 1933 work.	C xxx.	Semi-P.	Tribal.	1·8 miles × 2 miles.	S.	24,150			
	Block 6 Triangle clearing.	do. do.	D xxx.	Semi-P.	Tribal.	⅛ sq. mile approx.	S.	4,560			

TABLE 56.—*continued.*

Year	Name of the clearing	Purpose	Nature of clearing	Method em-ployed	Labour	Size	Settled or not	Labour in man-days	Contri-bution by the Tribe	Contri-bution by the Depart-ment	Total
									Shs.	Shs.	Shs.
			(*a*) In Shinyanga District—*continued.*								
1934	Kisapu clearing.	Continuation of 1933 work.	C xxx.	Semi-P.	Tribal.	Incomplete.	S.	6,520	1,100/00	10,204/00	11,304/00
	Ilola clearing.	do. do.	H xx.	Semi-P.	Tribal.	11 miles × approx. 1⅔ miles.	S.	14,420			
	Samuye Hills clearing.	Isolation of Block 7c and provision of a Cattle Corridor to the Manonga river mbuga system.	C xxx.	Semi-P.	Tribal.	4 miles × 1000 yds.	S.	28,930			
	Somageti/Wembere clearing.	Cattle Corridor to the Wembere Steppe.	⅔ F xx and ⅓ G xxx.	Semi-P.	Tribal.	3·4 miles × 1000 yds.	S.	8,410			
	Mihama river clearing.	Protection of Tungu river from fly.	H xxx.	Semi-P.	Tribal.	5 miles × 1500 yds.	S.	6,780			
	Salawe.	Cleaning up mbuga between Salawe and Sorwa with a view to reclamation of Sorwa.	H xxx.	P.	Tribal.	4 sq. miles.	S.	5,000			
	Clearing of thicket and bush on hard-pan in "Outer Circle."	Reclamation of "Outer Circle."	C x.	Semi-P.	Tribal.	3 sq. miles.	S.	2,760			
	Seke Tank.	Water for Huruhuru.			Tribal.	Capacity 350,000 galls.		4,680			
	Butuyu Tank.	do. do.			Tribal.	,, 700,000 galls.		4,000			
	Sayu Tank.	do. do.			Tribal.	,, 1,100,000 galls.		2,660			
	Half Way Camp Tank.	do. do.			Tribal.	,, 150,000 galls.		2,000			
	Miscellaneous.	Grass cutting, etc.			Tribal.			1,880			
			(*b*) In Maswa District.								
1932	Masinde river (Marialuguru) clearing (including Game Fence).	Reclamation of "Meat Rations Ranch," and freeing of Masinde river for the tribe.	½ C xx and ½ G xx.	P.	Tribal.	4·3 miles × 1320 yds.	Part S.	52,500	1,184/00	472/09	1,656/09
1933	Masinde river clearing.	Broadening of the 1932 clearing.	G xxx.	Semi-P.	Tribal.	3 sq. miles.	S.	25,289	1,000/00	427/90	1,427/90
1934	Mwasita clearing.	Completion of this Cattle Corridor to the Wida mbuga.	⅔ C xxx; ⅓ G xx; Part O.C.	Semi-P.	Tribal.	5 miles × 5000 yds.	S.	5,634	1,630/00	762/26	2,392/26
	Mwamwita clearing.	Cattle Corridor to the Wida mbuga and isolation of Dasina bush.	C xx, Part O.C.	Semi-P.	Tribal.	4½ miles × 1 mile.	S.	4,800			
	Chinamile clearing.	Cattle Corridor to Simiyu river and isolation of Nunghu Block.	⅔ C xx, ⅓ G xx.	Semi-P.	Tribal.	1·4 miles × 1 mile.	S.	32,000			
	Duduma clearing.	Cattle Corridor from Duduma mbuga to Simiyu. Isolation of Duduma Block.	⅔ C xx, ⅓ G xx.	P.	Tribal.	2·4 miles × 1 mile (not quite completed).	S.				
	Mwamwita Tank.	Water for Wida mbuga.			Tribal.			2,000			

			(c) In Kwimba District.								
1933	**Buhungukira.**	Reclamation for settlement and grazing.	½ D xxx, ½ E xxx.	P. and Semi-P.	Tribal.	Approx. 35 sq. miles, including much open country.	S.	186,500	12,000/00 (approx.)	2,215/41	14,215/41
1934	**Buhungukira.** **Simiyu river.**	Consolidation of 1933 work. Opening of river to settlement and cattle.	D xx. G x, Part O.C.	P. Semi-P.	Tribal. Tribal.	 Approx. 8½ miles × 650 yds.	S. S.	56,000 35,000	2,840/00 2,200/00	307/20	5,347/20
			(d) In Mwanza District.								
1934	**Msalala clearing.** (Strictly *not* anti-tsetse clearing.)	Provision of a settlement area.	A xxx.	Semi-P.	Tribal.	1½ sq. miles approx.	S.	10,610	nil	250/56	250/56
			2. *In the Western Province.*								
			(e) In Nzega District.								
1934	**Ngurube clearing.**	Stopping of tsetse advance eastward.	F xxx, Part O.C.	Semi-P.	Tribal.	2½ miles × 1 mile (not yet completed).	S.	5,510	3,000/00	150/00	3,150/00
			3. *In the Central Province.*								
			(f) In Kondoa District.								
1934	**Kikore river clearing.**	Isolation of block to be reclaimed.	G xxx.	Semi-P.	Tribal.		S.	1,800	600/00	117/00	717/00
			4. *In the Northern Province.*								
			(g) In Mbulu District.								
1934	**South Galapo clearing.**	Isolation of block to be reclaimed.	G xx, Part O.C.	Semi-P.	Tribal.		Part S.	10,755	600/00	120/00	720/00

(h) Summary as regards man-days and money contributions towards reclamations in all districts over the years 1931–1934.

	1931	1932	1933	1934	Total	In Shinyanga District alone.	In all other Districts.	**Totals.**
	Shs.	Shs.	Shs.	Shs.	Shs.	Shs.	Shs.	£
(i) Monetary contribution by the Department	6,494/81	29,899/21	9,773/29	11,911/02	58,078/33	54,324/89	3,753/44	8,711.15
(ii) Monetary contribution by the Tribes	200/00	1,907/00	14,100/00	11,970/00	28,177/00	3,123/00	25,054/00	4,226.11
	6,694/81	31,806/21	23,873/29	23,881/02	86,255/33	57,447/89	28,807/44	
i.e. £ *s. d.*	334.14.10	1,590.6.3	1,193.13.3	1,194.1.0	4,312.15.4	2,872.7.11	1,440.7.5	12,938. 6

Total man-days of Tribal Labour employed over four years 734,209 man-days.
Total of Paid Labour employed over four years 191,493 man-days (approx.).

Explanations :—A = Broad-leafed Savanna Woodling on eluvial (*Combretum Zeyheri, Commiphora Fischeri* and *Ostryoderris Stuhlmannii*). B = Thorn-bush of Acacias (especially *A. Benthamii*) and much *Dalbergia melanoxylon*. C = Open thorn-bush country composed of acacias (*A. spirocarpa*) with Commiphoras and *Lannea humilis*. D = Denser thorn-bush than B and composed chiefly of scattered *Commiphora* thickets with *Acacia* trees *not* an outstanding feature. E = More mixed thorn-bush composed of *Acacia spirocarpa*, scattered *Commiphora* thickets and much gall-acacia. F = Low-lying thorn-bush on an annually flooded plain, characterised by dense *Acacia Kirkii* and gall-acacias with island of C. G = Dense thorn thicket composed mainly of Commiphoras and Grewias but with scattered large acacias and in some cases a *strip of riverine* forest. H = Mbuga fringe with promontories of C, bays of gall-acacia and open spaces, alternately. x = Light bush of its type. xx = Medium bush of its type. xxx = Heavy bush of its type. O.C. = Old clearing with regenerating bush in it. P. = So-called "permanent" method of clearing employed. T. = "Temporary" method of clearing employed S. = Settled.

3.—PARTICULARS OF CLEARINGS.

(maps 2 and 3.)

A list of the clearings carried out in all districts and brief details as to purpose, nature of clearing, method employed, size, whether settled and cost, is given on pp. 358–361 in the form of a table. The "notes on the clearings" that follow it will amplify this information, as will, still more, the fuller details of some of the schemes given later (*see* pp. 366–399 below). The west Shinyanga scheme * has been dealt with so fully as a whole in other places that the clearings which have formed a part of it, though listed below, are not all discussed individually. The Huruhuru scheme, included in it, is described with other schemes under the section entitled "the scheme for opening up the greater mbugas" (*see* p. 384 below). The attack by non-burning on four blocks of bush in Maswa is included in no. 5 of sub-section C, on p. 376 below. For convenience some of the earth tanks made by tribal labour are included in the following list. It is difficult to separate reclamation from the surveys which necessarily precede it, and the sub-section on "the fly situation and schemes in Mbulu District" which actually is included below might equally have figured under "surveys."

B.—NOTES ON THE CLEARINGS.

(maps 2 and 3.)

1.—THE 1931 CLEARINGS.

The year 1931 was the first in which, after the temporary removal of the work from our hands, alluded to on p. 10 above, we resumed fully (with Napier-Bax, Senior Field Experiment Officer, in charge) the programme of reclamation, experimental and other, laid down in 1923–24. The interval referred to had seen a falling-off in the art of making clearings, but this was speedily remedied. Wheeler, Moggridge and F. H. Smith (the latter under the Administration) supervised the work. It was a bad locust year, and the tribe had been out for long periods on the work of destroying hoppers. It was therefore not thought fair or advisable to call on them again. In all, only 1,500 tribesmen came out, but the Tsetse Research Department employed paid labour.

The following gains were obtained for the experimental work. Blocks 4A and 4B, the former the site of our first and important experiment in not burning the grass, the latter the control block, were isolated. The southern end of one of these offered a further opportunity for demonstrating the effect of fire on *Dalbergia melanoxylon*. Not felled but merely ring-barked and piled, these trees burned out well.

The gains for the tribe may be summarised as follows :—

(1) In the first place Block 5A was isolated. This was the block which it was proposed to attempt to reclaim. A previous attempt by the tribe to make this clearing had been so badly carried out that we found it impossible to see how far the original clearing extended, full as it was of large *Ostryoderris* and other of the more hard-wooded trees and of thicket—all left because more difficult to cut. Even this year's clearing, however (breadth 800 yards, pl. 18, fig. 1), though well done, was still insufficient in width. Settlement was admitted in 1932. It is still confined to the ends, but is creeping up strongly through Block 5A, in which also cattle are grazing.

* *See* map 2.

(2) Secondly, protection for the native cattle was afforded in Block 3 from the flies in Block 4B.

2.—THE 1932 CLEARINGS.

(a) The Shinyanga District.

The staff consisted of five temporary European Reclamation Assistants (Messrs. Gabbutt, Vane, Nelson, Lyons, and Lombard), who were engaged for Shinyanga, and a staff of temporary native supervisors (nyamparas) at 12*s.* a month were engaged as an addition to our efficient permanent staff of native supervisors.

A large gang of paid labour was employed during much of the year in accelerating the task of breaking the bush up into blocks for our experiments, in making a start with our discriminative clearing experiments (in Block 5 and the "Outer Circle"), in making the fire-breaks (totalling 118½ miles) and 52 miles of road, and in erecting fences for a special experiment in the width of clearing that tsetse will cross. In addition, 5,800 unpaid tribesmen came out and worked under our supervision for ten days on the aspects of the scheme that immediately interested the tribe. The Senior Field Experiment Officer ended his report for the year by saying "the quantity and quality of this year's output is such as will not in future years be easily excelled."

The following gains were secured for the tribe in Shinyanga.

(1) Chibe kopje and its surroundings, forming an important salient and a capture much valued sentimentally by the tribe.

(2) The completion of the clearing of the "Beda corridor," leading to the Huruhuru Plains. This was the biggest tribal effort of the year.

(b) The Maswa District.

The big Marialuguru salient in which the fly projected into settled country was cut off from the main fly bush to its east by means of a clearing 1,300 yards wide. Wheeler was in charge of the work and the Administration and Agricultural and Veterinary Departments all contributed officers to help in the supervision. The details of the scheme and the results are given, with a map, on pp. 336–370.

3.—THE 1933 CLEARINGS.

(a) The Shinyanga District.

Findlay was mainly occupied on survey, but supervised clearing also. Lombard worked on clearing until incapacitated by illness. Two temporary Reclamation Assistants only were employed (R. T. Vane and H. J. F. Nelson), the work being more spread out chronologically than previously, but a staff of about 40 nyamparas was engaged—in most cases re-engaged—to assist in the supervision. The fact that "piling" (fig. 27 on p. 408) figured little in the 1933 programme permitted some economy here.

The policy was adopted of laying out the clearings in the preceding wet season. This avoids what has sometimes been a source of delay. It was suggested usefully that a collapsible ladder fitted to the strengthened roof of the cab of the lorry would, by raising the observer 15 feet, greatly facilitate this work.

Over 10,000 men turned out for 10 days for work against tsetse in the Shinyanga District. This, as the Assistant Director suggested, was "most satisfactory, remembering that this is not a district which is making its first great effort against fly but one in which reclamation work has been in progress

for nearly nine years." Numbers, discipline, and punctuality showed great improvement over those of the previous year.

The following clearing work was carried out on the Tsetse Research Department's plan of campaign for western Shinyanga. This was all in relation to the opening up of the great Huruhuru Plains.

(i) The entrance to the Beda cattle corridor which lies east of Old Shinyanga (*see* map 2) was cleared up for the benefit of the chiefdoms of the eastern cultivation steppe.

(ii) Four gangs of 500 men each were engaged on the clearing of the gall-acacias fringing the Huruhuru and Mwalukwa mbugas (*see* map 2) in order to create a fly barrier between the extensive gall-acacia woods of the plains and the fly bush proper. At no point was the clearing narrower than 1,200 yards. Mostly it was much wider, but the work was light and easy.

(iii) The northward corridor, two miles wide, into the Huruhuru system from the south-eastern cultivation steppe of the District (Lohumbo, Tinde, Usule and Usanda chiefdoms, *see* map 3) was begun. The clearing was carried into the bush for a distance of three miles.

In addition two important pieces of water conservation work were carried out, to be referred to elsewhere.

The following clearings were carried out in the various chiefdoms by special request under our direction. The practice of dissipating the tribal effort in small clearings of purely local interest and little value that had come into vogue in Shinyanga and which has been referred to on p. 11 above, had resulted in the production of numbers of clearings that were badly done through the impossibility of adequate supervision and some of which, recleared at our own expense after our return to the scene, were found to be almost indistinguishable from the virgin bush adjoining and full of fly and unusable. It was natural that the chiefs and people should not wish their work to be wasted and that our direction became in demand. The Mhumbo river clearing, carried out by Findlay in 1932, was of this kind and in 1933 we responded by surveying, selecting the sites for and supervising the following clearings :—

(1) A continuation of the clearing of the south Mhumbo river for Chief Makwaia of Usiha, under the supervision of Moggridge, who noted the possibility of breaking into a great mbuga in the south of the district and did so (fig. 26), with the result that many thousands of flourishing cattle have since found grazing there; * (2) a clearing for the Usanda chiefdom; (3) one for Uduhe at Kisapu; (4) one for Lohumbo at Ilola, each being merely the first instalment in a several years' scheme laid down by us and appreciated by the chiefdoms concerned; and (5) clearings for Salawe, Mondo, and Seke with the objects stated in the table.

Discriminative clearing went on. This had been carried out as early as 1924 in Block 1 in conjunction with organised grass fires, but the present was the beginning of an attempt to see whether, without the latter, discriminative clearing would be useful. The Ndama stream in Block 5 was cleared as an important instalment in this connection and thicket clearing took place in Block 5A and the "Outer Circle." The subject has already been referred to more fully on pp. 262–270 above.

In this year large gangs of paid labour were not used owing to a comparative shortage of funds.

* As the Assistant Director said in his report on the subject, "this was an excellent example of the useful additional work that can be done in the various chiefdoms under skilled direction."

(b) The Maswa District.

The Masinde River Clearing at Marialuguru * was broadened in May to a total width of two miles under the supervision of Findlay with Mr. F. Nuttall-Smith, Assistant District Officer. Messrs. Clissold and Ludicke were engaged by the Administration to help in supervising the operations. Settlement here has hitherto been prevented by a curse laid on the clearing by an old woman. It is essential, however, that settlement should come in for the prevention of the regeneration of the considerable areas of thicket that were previously present.

(c) The Kwimba District (Buhungukira).

(fig. 25.)

Wheeler was in charge here, assisted by Mr. C. Kostelesky. At times the Administration found it impossible to arrange for one of their own permanent officers to be present, as was the initial arrangement, and at their request Wheeler took full charge of the work.

As regards labour, 18,650 labourers were employed for the usual ten days.

A corridor 2 miles long and 1½ miles broad was cut into the area, a strip of thick bush at the foot of the hills over 5 miles in length and ½ a mile in width was felled for settlement, and the mbuga lying between the Mhalo and Mhande ranges, some 30 square miles in extent, was cleaned up.

4.—THE 1934 CLEARINGS.

(a) The Shinyanga District.

Findlay helped till he went to the Mbulu District. Lombard remained in Shinyanga throughout except for one month during which he was lent to the Administration to supervise anti-famine planting and (later) the supervision of the clearing in Nzega. Messrs. Robbie and Ireland, temporary Reclamation Assistants, from late May to early September and November respectively, distinguished themselves by hard work. "Nyamparas" were employed temporarily as in previous years and justified the expenditure involved, which amounted to Shgs. 2055/-. It is noteworthy that quite a number of these men are finding their way to the permanent service of the Department as vacancies occur.

Over 13,000 tribesmen worked their term of 10 days.

In	1931	1,578	men	worked	10 days.
,,	1932	5,442		,,	,,
,,	1933	10,163		,,	,,
,,	1934	13,398		,,	,,

The remark of the Senior Field Experiment Officer quoted for 1932 (p. 363 above) has been applicable in each subsequent year.

The tribe's contribution to its side of the general scheme in connection with the Huruhuru scheme was as follows :—

(i) The west end of the Beda corridor was broadened, the barrier clearings separating the gall-acacia wooding of the Huruhuru Plains were broadened and lengthened, Butuyu (*see* map 2, north) was cleared, the water supplies of the mbuga system were developed and consolidation generally was carried out. Sayu, an island of gall-acacias, which, owing to its position, wedged in a narrow bay in the fly bush (*see* map 2 and pl. 12, fig. 1) and having a greatly

* *See* fig. 24.

used path running through it, was constantly suffering re-infestation, was cleared altogether.

(ii) The two-mile-wide clearing that it is intended to continue from Usule to the Sayu " bay," both to form a corridor for cattle and to be a barrier against re-infestation by flies from the west of the general area which we are reclaiming for the tribe, was carried further northward than is shown on maps 2 and 3. Clearing was started at its northward end also, opening up pools on the Ningwha river for the cattle grazing in the Huruhuru.

Another clearing in the plan of campaign for western Shinyanga was the " Block 7c clearing" (Samuye), marked on the map as "probable clearing for 1934." This was duly carried out by Robbie, both to act as a corridor for cattle to the mbugas of the Manoga river and to separate for reclamation Block 7c which is needed for grazing.

We come next to the scheme for eastern Shinyanga. The Somageti–Wembere Clearing was the opening clearing of the campaign against the eastern Shinyanga fly belt. This clearing, which is designed to make fly-free the existing cattle-track from Somageti to the great, open Wembere Plain, will also, when completed, have the effect of leaving the very large block of fly bush near Kitalala (map 3) isolated for attack by ourselves.

Finally the following clearings were executed in the various chiefdoms by special request under our direction.

(i) The Mihama clearing, at the request of Chief Makwaia, to safeguard a drinking-place for cattle on the Tungu river and gain the riverine strip for grazing; (ii) the extension of the Ilola clearing of last year, which is expected to result in a large amount of grazing in return for a relatively minor effort; (iii) the continuance of the Usanda clearing of last year; (iv) the continuance of last year's Kisapu scheme, where before more work is done it will be necessary to get settlement into the area already cleared, otherwise effort will be wasted; and (v) a Salawe clearing constituting a first step in the isolation of Sorwa " Island " (map 3) from the main fly bush, for later attack.

As the fly position in Block 5A was becoming extremely unsatisfactory in certain sections, it was decided to make a start on clearing with paid labour the hard-pan patches of their remaining bush other than the large trees. The work was begun in September and extended into October and was directed chiefly to clearing the Majimera stream. Here all hard-pan and semi-hard-pan was very thoroughly dealt with. The result was a spectacular fall in fly in this section. The work ceased through lack of funds but has since been continued.

Apart from the considerable clearings made, some of which act as corridors to grazing and water while much of them also may be settled, the main gain for the tribe was the throwing open to settlement of the Outer Circle (*see* map 2) as the result of discriminative clearing and burning, although it was shown that discriminative clearing alone would have sufficed to produce the effect (*see* p. 269 above).

(b) Other districts.

The work in these districts is sufficiently covered in the next sub-section.

C.—DETAILS OF SOME OF THE SCHEMES.

1.—THE MEAT RATIONS COMPANY'S RANCH IN THE MARIALUGURU SALIENT, IN MASWA, AND THE TRIBAL LAND ADJOINING.

(fig. 24.)

Marialuguru, or Maria, forms a broad, deep salient jutting west into heavily-populated cultivation steppe from the great *swynnertoni–pallidipes* fly area,

the western margin of which runs from the Manonga river to the Speke Gulf. In it, together with tribal land, lies the ranch of the Meat Rations Company in Mwanza, the operations of which, in effect, form part of the machinery for reducing the cattle and the erosion which they cause in Shinyanga and Maswa. The salient was infested with *G. swynnertoni* and with a few *G. pallidipes* and we were asked to recommend measures.

Napier-Bax spent the first half of January 1932 in the salient, and studied the position thoroughly and made recommendations.

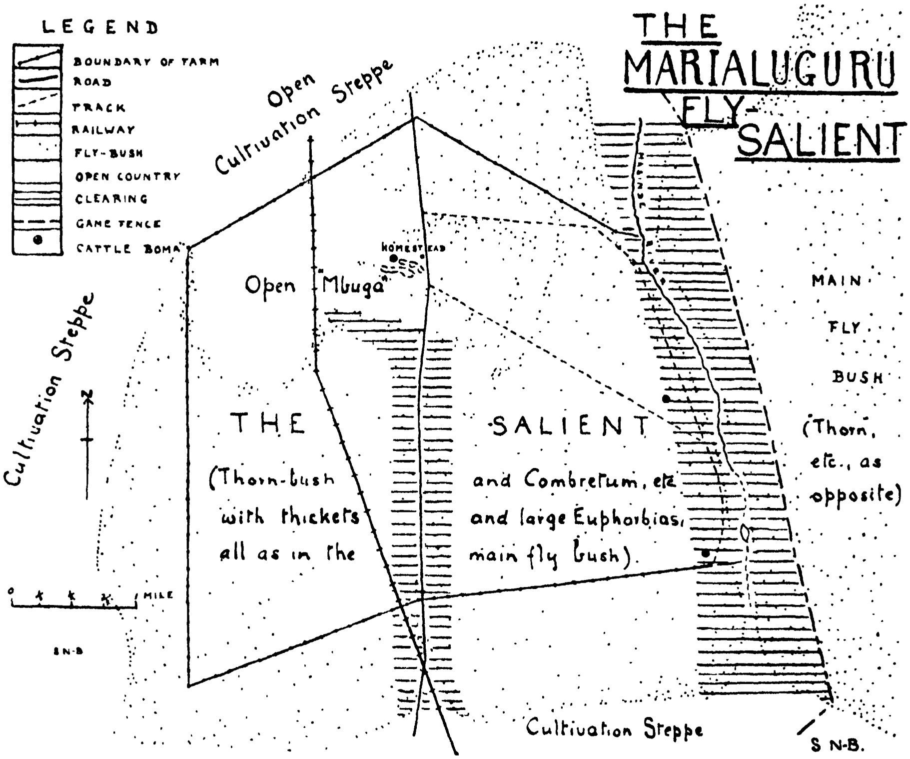


FIG. 24.—Sketch map, showing the Marialuguru fly-salient, cleared of *G. swynnertoni*.

As regards the vegetation, " The most striking vegetational feature of the concession is the number of Candelabra Euphorbias. These nearly always form the nucleus of small or large thickets. The larger type of savanna tree, with the exception of *Albizzia hypoleuca*, is almost entirely absent over great parts of the farm, in its mature form. The presence of deserted native shambas, ' Manyara ' (*Euphorbia Tirucalli*) and hedges and trees of *Cassia siamea* point to the fact that much of this area was once inhabited by natives and large stretches of regenerating bush bear this out.

" The bush immediately bordering the Masinde river is light, but some dense thickets extend to within a short distance of the river on its eastern side. . . . Generally speaking, the bush is denser along the whole southern boundary of the concession while it tends to become lighter towards the north. Other common trees and bushes include acacias (' gall-acacia ' or ' ilula ' including *A. seyal*), *A. senegal*, and occasionally a larger savanna *Acacia* not identified : *Dichrostachys*

sp.; *Grewia* sp.; *Commiphora* (*pilosa, Schimperi, Fischeri,* and *subsessilifolia*); *Fagara* sp.; *Lannea humilis*; *Kigelia* sp.; *Dalbergia melanoxylon*; and some very fine Tamarinds. . . . There is no reason why *G. swynnertoni* should not become firmly entrenched both in the virgin bush and the older regenerating bush. Further, this thicket type of country is ideal for *G. pallidipes*" (Napier-Bax, 21.i.32).

"Game seen on the farm were zebra, impala, dikdik, steinbuck, Bohor reedbuck and wart-hog. A single young roan and a Thompson's gazelle were also seen on the eastern side of the Masinde river. There was much kongoni spoor, but no kongoni was actually seen. The writer is informed that an invasion of game from the eastern side of the Masinde river takes place in the long rains. Most game and spoor were seen on the eastern side of the concession, but the whole area is evidently traversed by game, and zebra were actually seen within a few hundred yards of the homestead. Many lions accompany the alleged invasion of game in the long rains and cause much trouble to the cattle."

As regards the flies, "Examination revealed that the main bush on the eastern side of the Masinde river carried fairly dense fly. Fly was also found, albeit in lesser numbers, along the western side of the Masinde river. The remainder of the concession carries very light fly, except in the south-west corner where they are more abundant. One fly was actually taken in the cattle boma at the homestead, and three more within a hundred yards of it. Sparse fly are to be met with on the Malampaka–Nyambiti road where it passes through the bush promontory.

"The species of fly incriminated are *G. swynnertoni* and *G. pallidipes*. The former, however, is apparently much more abundant than the latter. Only four of the latter were taken, but the widely separated points at which these four were captured suggest that their distribution is wide. It must be borne in mind that *G. pallidipes* do not show themselves in their true numbers to man.

"There is no doubt that the main source of infestation is from across the Masinde river and that man, game and cattle have contributed to bring fly into the promontory. The spread of the fly has been aided by the very favourable vegetational environment in the concession area, and even if it has not yet secured a firm footing . . . there is a very grave danger that it may soon succeed."

TABLE 57.

Cattle losses on the Marialuguru Ranch in Maswa, believed to be due to Nagana.

Month	Number of cattle on farm	Deaths
1931.		
August . . .	1,187	5
September . . .	1,250	10
October . . .	1,221	33
November . . .	591 *	50
December . . .	340	4

* In October the cattle were moved to the homestead and during November many cattle were sent away from the farm.

The recommendations submitted by Napier-Bax were as follows:—

(i) "prevention of further influx of fly.

(ii) " starvation of the fly within the area by the exclusion of cattle and game. A game fence to be made along the whole length of the clearing.

(iii) " encouragement of grass growth (which is inimical to fly) by the exclusion of fire until the end of 1933.

(iv) " the burning of the preserved grass at the end of 1933, should that still appear necessary or desirable.

(v) " the slashing of the larger thickets on their south-eastern sides so that an accidental fire, or our fire of 1933, may make a relatively clean sweep; the exclusion of all cattle until the end of 1933; the erection of the game fence referred to above and the shooting and harrying of the larger game.

" In the meanwhile, pending the clearing of fly from the eastern half of the farm, the company's cattle would graze on the western side " (Napier-Bax).

In my covering letter the recommendations were recapitulated as follows :—

" As regards cutting off the flies from reinforcement, it is absolutely vital :—

(i) " that a clearing not less than three-quarters of a mile wide should be made along the Masinde river, mainly on its east side. This is the very minimum possible in view of the fact that *G. pallidipes* is present. . . .

(ii) " *that it should not be settled* (unless it is made at least two miles wide). This in relation to *G. swynnertoni* [*see* p. 306 above].

(iii) " that it should be combined with an adequate game fence, and its shoulders be similarly protected, to help keep out the annual and sporadic game influxes.

(iv) " that the fence should be on the east (main fly-bush) side of the clearing and be well protected from fire, but the clearing be well burned through annually to keep any re-growth down.

" As regards the extermination of the flies already on the farm it was vital (*inter alia*) :—

(v) " that the farm be sub-divided by a half-mile-broad clearing (on an easy line indicated by Napier-Bax).

(vi) " that the cattle be kept off the ground to the east of the road till the end of 1933.

(vii) " that a system of fire-breaks and traces be instituted by the farm management under our advice.

(viii) " that grass fires be excluded absolutely—at least till we give the word, which will not be before September, 1933. We find a prolonged long-grass period inimical to the flies.

(ix) " that, against the case of fires taking place or an ultimate decision to burn, the south-west sides of all important thickets east of the road be slashed and passages be slashed through the larger of them.

(x) " that the position be watched by my Department and any modifications to these measures which may from time to time be found necessary be put into effect by it or on its recommendations. Thus any tendency on the part of the flies to concentrate or form feeding-grounds might be used as an opening for attack.

(xi) " *Game* : it should be quite unnecessary to shoot such localised game as kudu, impala and steinbuck, but the wandering game should be driven out by shooting when it outflanks the fence.

" I am exceedingly hopeful of clearing this land of ' fly ' fairly quickly."

A clearing 1,300 yards wide was made under Wheeler's supervision in 1932. The width was doubled by Findlay in 1933 to two miles and native settlement

was admitted. The thickets were slashed and the grass fires controlled. On September 1st, 1933, the whole of the area to the east of the road was burned by Vicars-Harris and Vane, a good burn being obtained. No killing of game took place and it did not prove necessary.

Fly rounds were instituted from the start and fly boys were sent to carry them out every fortnight. An occasional visit was paid by an entomologist.

As a result, it is now long since any flies were taken in the salient.

2.—THE BUHUNGUKIRA PROBLEM, IN THE NORTH OF THE HURUHURU SYSTEM, KWIMBA DISTRICT.

(fig. 25.)

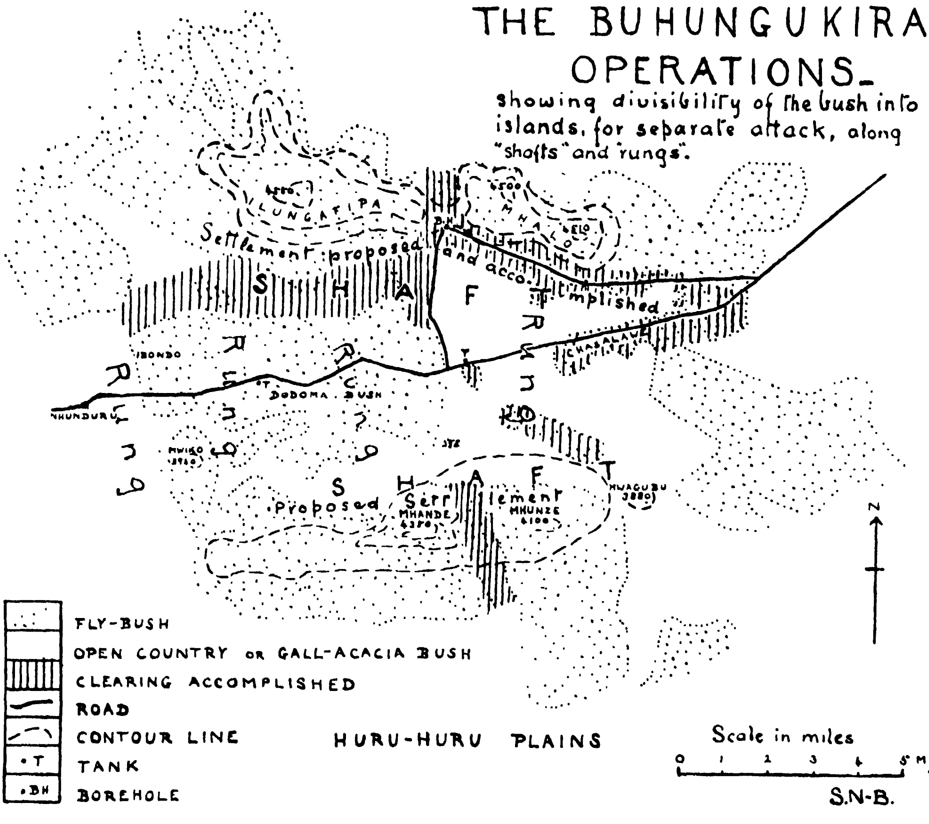


FIG. 25.—The Buhungukira operations, showing divisibility of the bush into islands, for separate attack, along "shafts" and "rungs."

I carried out an investigation for the devising of a reclamation scheme as the result of a request from the District Officer. The following are quoted from my report :—

" History. The problem is a very simple one and my work was further facilitated by the fact that the area is not new to us. My head fly boy, Swedi, was sent by me in 1923 to investigate and report on it and he re-accompanied me now; Mr. W. H. Potts, now Senior Entomologist, accompanied by Mr. H. S. Magnay, again investigated the fly distribution in Buhungukira in January 1926. The only apparent change that has taken place in the latter since these events has consisted in the invasion of the ' island ' of Mhande."

The Position.

"(1) South of the Ilangafipa–Mwamani Range.

"The great mbuga system of which the Huruhuru is the south-eastern corner, lies, as to its north, in Buhungukira and Nera, both in the Kwimba district. In the former chieftainship this mbuga system is bounded on its north by one side of the wedge-shaped range of hills referred to in the heading, this side of the wedge descending into the plain on a line three miles north of the present water-boring camp of 'Dodoma,' on the Salawe–Runere road. North of these hills lies the main *morsitans* fly belt of the district.

"A strip of fly-infested bush, apparently mostly by no means dense, and from 300 to (probably) 1,200 yards broad, fringes the southern foot of the hills on a band of good, well-drained brown soil that completes the slope to the northern edge of the general mbuga system. *This fringe is important for future settlement should water be supplied.* The brown soil, the black (mbuga) soil and the intermediate soil provide opportunities for growing successfully a fine range of crops.

"*The band north of the road*, six miles wide, lying next to the brown-soil fringe under the hills referred to above, may be compared to a ladder. The shafts of the ladder (running roughly from west to east under the hills) are mbugas; its rungs (running north to south, some of them as wide as their interspaces) are (*a*) bands of open cultivation steppe (the two, that is, on the east, namely Tunduru and Maboko's, and that on the west, namely Sanga); or (*b*), mbuga (two bands between Maboko's, and Sanga). The western interspaces are relatively small islands of fly bush proper, containing much thicket. . . . Both *morsitans* and *swynnertoni* are present, the former in numbers. The eastern interspace (Upamwa to Sanga) is typical *swynnertoni* bush, contains that fly, and is good burning country.

"*The far deeper band south of the road* contains three large fly-bush 'islands.' These from west to east are Mhande, a narrower 'island' which contains the villages of Magubu and Sikubiji, and a far larger 'island,' further east and extending far south, which comprises the bush-area of Mwavarumbaga and (to the south) perhaps Mwakaburi (map 3). The Mhande 'island,' from the big hill on which an excellent view of the problem can be obtained, will not burn well, whether as a result of the locusts having eaten the grass or as a permanent condition I am unable to say. Most of the bush is not dense, but it is practically connected at its west end, through the Mwiko bush-area, with the Ibondo bush island of the band north of the road. Mhande is infested with *G. morsitans* (*G. swynnertoni* may be present but was not seen), Mwavarumbaga–Mwakaburi with *G. swynnertoni*. The islands contain excellent soil and the 'shores' of the islands, the north shore in the first place, are potentially important for settlement. The greater part of all the mbugas referred to is clothed thinly or thickly with gall-acacias. While these are not a favourable type of bush for the fly they tempt the latter into and across the mbugas and render the latter unsafe for cattle. Gall-acacias are easy, cheap clearing. A man clears half an acre a day even where they are dense.

"(2) North of the Ilangafipa–Mwamani Range.

"The Salawe–Mwanza road running north-west, more or less, joins up the ends of the 'L,' or wedge, of the hills. . . . In the irregular triangle between the road and the hills are at least four broad mbuga-heads, which, narrowing, cross the road and then turn more or less down its west side, south-westward.

The combined mbugas, on reaching Mount Sisu, pass along its north side westward into the Sanga river, which running north, enters Smith's Sound [of Lake Victoria]. The mbugas contain much ilula. Between the mbugas and between the road and the hills are areas of close bush containing a good deal of thicket and thoroughly infested with *morsitans*. These will not, for the most part, burn well and the bush is of a type that is relatively expensive to clear. North-west of the road the *morsitans* infestation continues.

" Recommendations.

" 1932. (i) No scheme can be undertaken without ample water. If boring fails to provide water, or in any case, if trial man-pits, dug now, or an earth-auger, should show ample depth of good clay, I would suggest digging a series of storage tanks for water in the mbuga-clay soil south of the brown-soil fringe along the south foot of the hills, and another series off the north shore of Mhande. Enough of these to supply the labour and first-year's settlers with water should be made this year. At any rate by some means provide water.

" 1933. (ii) Clear by ring-barking all the ilula of the shafts and rungs of the ' ladder ' between Mhande and Mwagubu ' islands ' on the south and the hills on the north " [fig. 25].

" (iii) Widen to 1,200 yards at least any of these clearings that are less than that distance across, break, at least equally broadly, the ' Mwiko ' connection between the west end of the Mhande bush-island and the Ibondo bush-island, and clear completely all bush that is even semi-ilula [gall-acacia] south of the road.

" (iv) Incidentally to such widening or otherwise, clear back, to 500 yards at least, the brown-soil fringe along the south of the hills—as much of this as can be settled—and along the north ' shore ' of the ' island ' of Mhande. Clear back from the road to a similar distance between Upamwa and Sanga.

" (v) If labour suffices, clear up or reduce one or more of the bush-islands between the road and the hills.

" (vi) Hold up all grass-burning in the general area concerned. A big organised fire could take place in 1934 if the state of the grass warranted it, or prohibition of burning could continue as a reducer of fly.

" (vii) Provide further water.

" Measures (i), (iv) and (vi) should provide you with good ground and water for two long lines of settlement, facing each other across five to six miles of grazing, the first along the southern front of the hills, the other along the north of Mhande ' island.'

" (ii), (iii) and (v), will (α) provide a large open grazing area between these two settlements, (β) isolate all the fly islands—large ones and small ones—that have been left uncleared. These will then be innocuous provided they are not closely approached by cattle, and can be dealt with individually. The general hold-up of fire should in any case tend to diminish the flies contained in them."

The programme for the subsequent years is given in sufficient detail in the summary to my report, as follows :—

" 1. The fly bush of south Buhungukira, for, say, twelve miles back from the edge of the main great mbuga, taking this to commence south of Mhande, is divided up into islands and strips by means of bands of black-soil mbuga.

" 2. These bands are for the most part clothed in gall-acacias (ilula). Ilula trees are cheaply and rapidly cleared and their clearing in this instance would result in the opening of a very great many square miles to native

settlement and grazing. In places the clearing would have to be wider than the present width of mbuga.

"3. A five-year plan is suggested, but is dependent on the provision of water. The first year would see the clearing (except for fly islands) of a large oblong of grazing ground between the Ilangafipa hills and Mhande and of two strips for settlement facing on to this oblong from north and from south. The second would probably see the process extended to the 'Sengerema' mbuga system north of the hills. This needs rather fuller consideration. The third (I suggest) would witness a return to the plain with extended clearing and settlement round the large 'island' in the south of the district. The fourth and fifth would be devoted to the completion, consolidation and perhaps extension of the work and the additional provision of water.

"4. An attempt would be made by my Department to get rid of the fly in one or more of the smaller islands. With success, and funds available, the larger might later be tackled, but it would not spoil the general scheme if this were not possible or the attempt were not everywhere successful.

"5. As regards 1933 the following plan is suggested:—

18,000 tribesmen come out for ten days each in six successive bands of 3,000; the work commencing on April 26th and ending on July 10th. Mr. Napier-Bax visits the site beforehand and lays out the work. Mr. Napier-Bax and a Field Experiment Officer then go to Buhungukira on about April 15th, make all final preparations and start the work. The Field Experiment Officer is left to direct the work as at Marialuguru this year. Supervision would further be exercised by one of the Administrative Officers of the district, a Reclamation Assistant from ourselves and at least one more supervisor. Adequate native supervisors to be supplied by the Administration and tribe and (a few) by ourselves. All grass-burning between Mhande and the hills to be held up, the necessary fire-breaks being made."

The following work has been carried out. Findlay completed a detailed survey (covering 130 square miles) in April, 1933. Lloyd carried out an entomological survey. A large proportion of the programme for 1933 was carried out in that year by Wheeler, who deserves great credit for his handling of large masses of labour and for the result obtained. The full programme for 1933 was not completed in that year owing to failure of water supplies, but a fine and striking effect was obtained, an area of close on 50 square miles being freed of fly. Findlay continued his work in 1934, when a corridor was carried between the Mhande and Mhunze Islands. A break through was made to the "Sengerema" mbugas over the hills. In places where a fierce fire was obtained there was little regeneration. Much of the area was burned out in 1934, but the offender was captured and punished with, it is hoped, salutary effect, and much grazing still remained.

One of the bore-holes put down by the Geological Survey Department produced a fine water-supply and four earth-tanks have been made also. Settlement was held up for a time owing to delay with the bore-hole pump, but is now coming in well, and new tribal headquarters have been built for the chiefdom of Buhungukira at Nyahanga, not far from the site of the bore-hole. A large number of individual peasant holdings have also been laid out by Mr. MacGillivray, District Officer, the following quotation from a letter from whom of 26th June, 1934, is of interest. "Settlement at Chasalawe goes on

apace. We marked out 30 plots of 20 acres each and hedged with manyara the main roads through the plots. Twenty-eight of the plots have already been taken out on an understanding that individual tenure will be recognised in due course. The idea has caught on so well that Seagar is now busy marking out a further 70 plots. The total of 100 will occupy the whole of the old recognised village of Chasalawe. The marking out has now been completed and very nearly all the plots taken up. The " peninsula " is a most heartening sight, houses and cattle kraals going up in all directions."

With the new tribal headquarters located at Nyahanga the area will fill gradually and the remainder of the five-year programme will be carried out *pari passu*. It is proving that it will actually take longer.

The tsetse position in 1934 was as follows :—" In going over the work no fly were seen except in Dodoma ' island ' where the lorry was fiercely attacked. Yet the new road below Mhalo to the bore-hole was traversed twice, the hill to the east of the bore-hole scaled and the clearing there examined, the old road down to Dodoma dam was followed two or three times, a spur of Mhande was climbed, the southern corridor between Mhunze and Mhande was visited and finally the lorry was taken along the fire-break running close to the north side of the Mhunze bush " (Napier-Bax, report, 30th August, 1934).

In 1934 Findlay found flies still numerous and active on the west of the Mhande corridor and south-west and north-west of Nyahanga.

The following work was carried out in 1935.

Several thousand men worked on clearing and tanks. The Salawe road is much used by cars, people, and cattle, and there is a real danger of distribution of flies thereby out of the Dodoma bush. The clearing of the mbuga to its north (a still infested part of one of the shafts of the ladder referred to above), with the diversion of the road into it, will meet this trouble. Certain other precautionary clearings are contemplated which will contribute to the completion and consolidation of the scheme.

Fire-control in the hills is likely to be difficult for a time as gold has been found there in places and prospecting is being undertaken.

It is proposed to dig several more earth-tanks for water (some for people and some for cattle) to serve the Chasalawe area and the stretch between this and the bore-hole.

As regards settlement, steps are being taken to populate the ground at Dodoma camp and elsewhere on the north of the clearing. A dispensary and dwellings for several native officials are to be built here. There will still remain much ground even here which will be available for settlement generally.

A further survey of the tsetse position will be useful in 1936.

3.—MIHAMA AND THE TUNGU RIVER.

(map 3.)

This survey was carried out by Vicars-Harris in April 1934, with the object of formulating a scheme for freeing the Tungu river from fly so that cattle could water there and for preventing the spread of the Kitalala fly across the river.

The boundary of the real fly bush on the east appeared to be the edge of the rather fine *Acacia spirocarpa* country, while thin fly extended across the mbuga lying between the Isanga and Semelo settlements to the edge of the dense riverine strip bordering the Tungu river. Odd flies are, occasionally, encountered in the country west of the river, but these are obviously wandering flies brought

across by man or game. No flies could be found in the riverine strip, and a later reconnaissance by Potts confirmed both this and also the fact that no *G. pallidipes* appeared to be present. The mbuga referred to is filled in places and merely crossed in others by strips of ilula (gall-acacia) wooding of considerable density. Many kinds of game are common during the dry season, these being concentrated on the Tungu river, while even in the rains herds of wildebeest and zebra roam the mbuga. Defassa waterbuck and Bohor reedbuck are almost permanent inhabitants of the riverine strip. Black rhinoceros are common during the dry season and lions abound. The promontory, for such it is, protruding from the Kitalala bush, is bounded on the south by the old Dodoma clearing, begun by Tcare and continued by the Administration in 1930 as a corridor for cattle from Mihama going to the Wembere via Kitalala; it is bounded on the north by cultivation steppe.

It was suggested that, by clearing the mbuga of all its ilula bush to a width of about a mile (*i.e.* to the edge of the *A. spirocarpa* country) fly would no longer come into direct contact with the riverine strip at the Tungu, and that it would be possible for cattle on the west side of the river to water with safety. It was proposed further that, by exclusion of fire from the riverine strip on the east side of the river that strip should be kept so dense as to exclude fly. Thus, even if odd flies crossed the cleared mbuga on man or game, they would not find favourable fly bush.

The clearing suggested was carried out in 1934 and completed with the exception of a very small patch of ilula at the north end which is not of importance. The riverine strip was protected from fire, but this was vitiated by the fact that we found it quite impossible to exclude cattle from the strip, with the result that it was heavily trampled and grazed in places. This may form a menace to the riverine strip and to the country beyond in the future, since if it becomes sufficiently opened it may gradually become infested with fly, and the cattle watering at the river may draw the fly gradually into the fly-free country beyond. As there is no legislation to prevent cattle entering this area nothing can be done for the moment (Vicars-Harris).

4.—SOUTH-EAST UDUHE AND SOMAGETI.

(map 3.)

Vicars-Harris reconnoitred this area also in April 1934, in order to study the fly position and ascertain whether there was any easy way of opening a corridor to the Wembere and of thus isolating the Kitalala block from the main Meatu fly bush.

In April 1934, the heavily grazed areas to the north of Uduhe and of Uchunga and Mwagala did not offer sufficient grazing for cattle. Considerable herds are sent to the Somageti area during the early dry season, but these are eventually evacuated from here owing to lack of both grazing and water and moved through the fly bush to the south to the Wembere at Hendawashi and thence eastwards towards the Semu mouth. In trekking from Somageti the cattle pass through about ten miles of lightly infested fly bush.

It was suggested that a corridor should be cleared parallel to the Somageti and Sanga rivers to the point where these two separate, the corridor thereafter to cross the former river and to follow south parallel to the Sanga river to the open steppe. This corridor, besides giving a fly-free passage for the cattle during their yearly trek to the steppe offers also excellent land for cultivation

and ample water for settlers, lying as it does along the common basin of the two rivers mentioned.

Work done. The corridor proposed was started in 1934 and continued in 1935. At the end of July 1935 it had been carried nearly out into the open steppe to a width of 1,000 yards.

As a result, there is now a corridor which should be more or less free of flies by which cattle can pass to and fro, and land is free for settlement. The clearing should, however, be widened to one mile as originally recommended and carried on right out to the edge of the steppe. In addition the Kitalala block is now isolated and can be used as an experimental block in the future.

During the rains buffalo infest the swamp between the two rivers, the place being literally trampled by them, while lions are common. During the dry season game becomes concentrated near the water, the commoner species being eland, roan, zebra, giraffe, Defassa waterbuck, kongoni, wildebeest, rhinoceros, Thomson's gazelle, impala, ostrich, and lion, while elephant visit the area from time to time. Smaller buck also are common. (From Vicars-Harris's report.)

5.—THE MASWA FIRE-EXCLUSION AREA.

(map 3.)

Various clearings had been carried out in the neighbourhood of this area since 1927 when the Tsetse branch of the Game Department started a break-through to the Wida mbuga and a clearing of the Simiyu river itself.* A "sleeping sickness clearing" runs north to south right through the area guarding the road, while the Mwamwita clearing from Luguru to the Wida had also been partly effected in 1928. Parts of the break-through from Mwasita to the Wida had been undertaken by the Administration during various years, but these clearings had only been partially cleared of trees, and in no case were they finished. On the west, a partly-finished clearing had been made to open the Chinamile pool, but this had been so incompletely accomplished that it was difficult even to identify the clearing. This was the position when Vicars-Harris came to do the survey of the District in October 1933 and recommend measures against *G. swynnertoni*.

It was obvious at a glance that the first thing to do was to finish off properly the clearings that had been left half done, viz. the Mwasita and Mwamwita corridors and the Chinamile clearing. In addition the natives wanted, so the District officer said, to break through to the Simiyu from the Dudumu mbuga. The site for a clearing was chosen and recommended. This was to run from the Dudumu mbuga to join up with the Chinamile clearing. The completion of these clearings leaves a big block of bush some 150 square miles in extent cut off from the main Meatu fly bush and cut off also from the Sengerema and Itilima blocks.

The clearings necessary to segregate this area were completed in 1934 with the exception of a section of the Dudumu corridor which was not quite finished. The block was then subjected to fire control, and with the exception of one comparatively small accidental fire was not burnt at all during 1934. During October 1934 a series of fly rounds were started to keep us informed as to the fly position and to give, we hoped, some information as to the behaviour of *G. swynnertoni* under these conditions. Additional rounds will be put in and the area will be surveyed botanically.

The area can be divided into four sub-areas, viz. the Mahaha, the Kimali, the

* This operation was interrupted by the event referred to on p. 10.

Dudumu, and the Nunghu Blocks. The Mahaha and Nunghu Blocks lie to the south of the Simiyu river and are the two smaller blocks. Of these the Mahaha Block has an old "sleeping sickness clearing" running diagonally across it, with a considerable settlement in the middle of it, and is much cut up by large open mbugas. Generally speaking, fly is very thin in this block. The Nunghu Block has quite thick fly and is very largely hard-pan country. These two blocks are separated from each other by the old road clearing already mentioned. To the north of the Simiyu lie the Kimali and Dudumu blocks, also separated from each other by the old road clearing. These blocks are considerably larger, being about ten miles long by five or six wide, and they are crossed in the north by a range of hills and kopjes which stretch right across them from east to west. To the south of these hills lie extensive mbugas and hard-pan areas, and, a feature of the area, considerable expanses of *A. rovumae* hard-pan country of a particularly fine type. The blocks are much split up by long open mbugas, especially the Kimali Block, while isolated kopjes, usually quite small, but completely detached from the main hill block, are scattered over the whole of the northern half of each block. The flies at the end of December were fairly thickly concentrated on the hard-pan flats near the Simiyu area, but detailed fly reconnaissances of the northern portion of the Kimali and Dudumu blocks had not yet been carried out. It is likely, however, that the hills are of importance and will be found to be heavily infested on their lower slopes, while the *Acacia rovumae* hard-pan seems likely to be equally important. Later reconnaissances of the area have confirmed this, while it was found that, during the very heavy 1934-35 rains, the Simiyu area became almost fly free.

Game becomes very heavily concentrated on the river during the latter part of the dry season. During the rains only certain species remain. The following are the principal species that concentrate :—impala, giraffe, Bohor reedbuck, Defassa waterbuck, bushbuck, roan (only a few during the rains), topi, zebra, eland (much reduced numbers during rains), lion (common in dry season), wildebeest (common in dry season), and small game of various species. (From reports by Vicars-Harris.)

Since the above was written, though the flies were already reduced, this valuable experiment and scheme has had to be abandoned, at any rate temporarily, through lack of local support.

6.—THE SCHEMES GENERALLY BETWEEN THE RAILWAY ON THE WEST AND THE RIVER SANDAI IN THE SOUTH, NORTHWARD OF THE FIRE-EXCLUSION BLOCK.

(map 3.)

These schemes also result from surveys by Vicars-Harris with the District Officer and Potts and they include (i) the re-clearing, at the desire of the people of Usmao, of the old "sleeping sickness clearings" following the Simiyu river, there being many trees standing in these, and both *G. swynnertoni* and (one) *G. pallidipes* being taken on reconnaissance by Vicars-Harris and Potts; (ii) the cutting of the corridor to Ntukusa mbuga which is referred to below, and which would assist the wish of the people of Ndagalo to return to their old tribal centre in the Lulongwa hills; (iii) a clearing from near Nyakabindi to a mbuga at the junction of the Sandai and Duma rivers, with a clearing along the Duma. These clearings were all desired by the natives, but the effect from the point of view of large-scale reclamation from tsetse, which is what appeals most to ourselves, is that, if carried out, these clearings will break the great block of fly bush between the Duma and Simiyu into four blocks—five including

Chinamile—which could then be attacked individually—by non-grass burning if the experiment to their south should prove as successful as we expect. The blocks are those of Ndagalo, Itilima-Ntusu, Sengerema, Chinamile, and Nyakabindi. The clearing on the Duma would have the further effect of giving a fly-free margin to this portion of the Serengeti Game Reserve. This whole piece of country was in 1923 the competitor of Shinyanga for our first experimental attack on tsetse, but Shinyanga was the site selected.

Half of the course of the Simiyu was cleared up in 1934 by tribal labour, under the supervision of Wheeler. The proposed Ntukuza clearing was marked out by the same officer, but has not yet been attacked.

7.—CENTRAL NZEGA, WESTERN PROVINCE, MAY–JUNE 1931.

The later surveys were undertaken at the request of the Nzega District Administration. The following is an extract from Jackson's report:—
" Central Nzega consists of a broad open area of cultivation steppe, grazed by large herds of cattle, and surrounded by low hills clothed with woodland of *Berlinia–Brachystegia* of a somewhat xerophytic type, lightly infested with *G. morsitans*. It is only since the war that this tsetse has occupied all the woodland in the east of the district, between Nzega and the open plains towards the Wembere steppe. Then the fly belts advanced round either side of the main central cultivation, joining forces in the eastern woodlands about 1924 and completing the encirclement of the District.

" All the available country has now been occupied by *G. morsitans*, and there is no danger of further major advances [by this fly]. The remaining problems are thus concerned with local increases of grazing areas, or with arresting the gradual retreat of villages on the periphery of settled areas, allowing the progressive upgrowth of bush on the margins and consequent slow encroachment of the tsetse. Particular attention was directed to such gradual encroachment in the eastern sultanates of Nyawa and Unyambiu, where the population were being steadily squeezed into smaller and smaller areas in this way, and a scheme was put up to arrest this inexorable process and to provide for progressive expansion of the settlements. In Bulundi, in the south, clearings were recommended to cut off wandering flies, sufficiently numerous to exclude cattle, from the true habitats on which they appeared to be dependent. It is understood that all these suggestions have had to be shelved owing to the financial depression." (Jackson.)

The following points are of special interest:—

" Three interesting points were noticed in the course of these surveys. One is a marked recession and reduction of *G. morsitans* in the great area of *Isoberlinia–Brachystegia* woodland lying between Tabora and Nzega on the main road, and also in the similar country southward and westward from Nzega and Bukeni. The process is attributed locally to an invasion of dragonflies early in 1931 " [and will in any case certainly be reversed].

" The second matter of interest was the rather heavy infestation in the east of a block of country about 20 miles across from which the genera *Isoberlinia* and *Brachystegia* are absent. The country is dominated by *Ostryoderris Stuhlmannii*, *Lonchocarpus capassa*, *Combretum Fischeri*, *Cassia abbreviata* and other broad-leaved trees.

" The third matter of interest is that throughout these areas game animals are rather uncommon, but the tsetse evidently finds them sufficiently numerous."

8.—NGURUBE IN NORTH-EASTERN NZEGA, WESTERN PROVINCE, MARCH AND JULY 1931 AND AUGUST 1933.

At the request of the Administration also, the Ngurube area in north-eastern Nzega was examined with a view to allowing the cattle of that place fly-free access to the grazing of the open Ukama plains. Jackson reported that: "It was found that *G. morsitans* was based on hills clothed with the broad-leafed trees just referred to, and that from these hills hungry individuals roamed out through thorn scrub lying across the route which it was desired to open to the plains. The thorn scrub included the gall-bearing *Acacia malacocephala*, with some *A. mellifera*, *A. Kirkii* and *A. pallens*, while gravelly rises supported *A. senegal*, and in one place there was an extensive tract of *Euphorbia matabelense* and *Commiphora campestris*. This last belt was rather avoided by the tsetse, and the suggestion was that a corridor one mile wide and five miles long might be cut flanking this belt, thereby reducing the pressure of flies on the infested side. Later (1933) *G. swynnertoni* was found to have spread along the Manonga river to Ngurube from the west, as indeed had been prophesied in 1926 by members of the Department."

There was further country, which *G. swynnertoni* might infest, though *G. morsitans* was unlikely to do so. This, then, was an instance in which *G. morsitans*, reaching its vegetational limit, had in effect handed the baton to *G. swynnertoni* in order to continue the advance, as in a relay race. In order to meet this threat the original reclamation scheme had to be modified and a one-mile **S**-shaped clearing was recommended for the division of the fly bush from country to the east, less favourable even for *G. swynnertoni*. In and behind this barrier it was recommended that the local population, reinforced by evacuated refugees from other fly areas, be encouraged to concentrate, thus barring off the spearhead of the advance down the Manonga valley.

Slightly under half the clearing was completed in 1934, but the Ngurube people took new heart and the retreat can be regarded as stemmed. It is planned to complete the work as soon as possible.

9.—THE CLEARINGS FOR THE PROTECTION OF THE MPAPWA VETERINARY FARM AND HEADQUARTERS, CENTRAL PROVINCE.

(fig. 23.)

Burtt's survey of Mpapwa and the results obtained have been fully discussed under the heading "survey" on p. 340 above.

In 1933, following Burtt's recommendations, clearings were made by the Administration across the Tambi river above its junction with the Matamondo river, and lower down across the Matamondo river itself. The clearings cut through the entire wooded strip on each side of the rivers from side to side and were made 1,100 and 1,200 yards wide respectively. In 1934 two more clearings were made. One was a mere continuation up the Tambi of the clearing of 1933 to a further width of 1,800 yards; the other cut across the Matamondo river to reach the Chankokoma river above its junction with the Tambi on a width of 750 yards. The object was to check the supposed seasonal advance of the tsetse, *G. pallidipes*, down the Tambi from its area of high infestation towards Kidete.

None of these clearings were "complete." The river-thicket and small trees were cleared but the larger trees were ring-barked only. Nevertheless both the native cattle and those on the Veterinary Farm at Tubugwe have been remark-

ably free from trypanosomiasis, following the 1933 and 1934 clearings. It is actually rather extraordinary that with the large trunks still standing *G. pallidipes* should have been checked in its passage. Work in further seasons including a new full entomological survey are necessary before the position can be fully assured. The clearings, meantime, are being consolidated, as they should be. I am indebted for the latest news on the subject to Capt. Lowe, Acting Deputy Director of Veterinary Services at Mpapwa, who has written to me on the subject, and to the District Officer, Capt. Wilkins, who has prepared a report.

10.—THE FLY SITUATION AND SCHEMES IN THE MBULU DISTRICT, NORTHERN PROVINCE.

(map 1.)

(a) The general position.

Mr. C. Gordon-Russell, formerly of the Tsetse Research Department, has now long been resident in Mbulu as Reclamation Officer to the local Administration. He has carried out good surveys and extensive and useful reclamation schemes. We have occasionally come in on consultation. On his being transferred to the Administration in 1934, with the expectation that his time for tsetse work henceforth would be limited, the Acting Provincial Commissioner of the Northern Province, Capt. C. McMahon, asked for our fuller co-operation and thereby made it worth while for us to re-open our station at Kikore, with Findlay in charge.

A broad bar of uninfested high country, varying from 15 miles in the north to 35 miles wide in the south, connects the broad Northern Highlands north and north-east of Ngorongoro with the country, still uninfested, of north-east Singida (*see* map 1). An arm of tsetse-free country is thrown from this strip eastward, up to and just including Babati and Mount Ufiome. In the base of the " bar," here 35 miles wide, lies the country of the Barabaig tribe, part below, part above the Rift Scarp and best settled around Mount Hanang. In the arm to the right live the Wafiome. In the rest of the strip, running north-north-east to Ngorongoro and 25 to 10 miles wide, lived formerly the Wambulu nearly up to the Endabash river. Following this stream a band of tsetse cut off all access to the north, but, since this has been traversed by corridors (*see* p. 398 below), the area occupied by this tribe now extends all the way to Oldeani. The band of tsetse on the Endabash (westward) consists of *G. swynnertoni* and *G. pallidipes* mixed, but Findlay reports taking many *G. morsitans* as well as *G. pallidipes* on and near the slopes of Mount Dum and between that hill and the cattle route to Bugeri further east. These have doubtless come up from Lake Manyara.

On the west side of the highland strip described as connecting north-west Singida with the Northern Highlands, lies a solid and very extensive belt of *G. swynnertoni* and *G. pallidipes*, occupying the west of the country of the Barabaig and Wambulu and enclosing both the Yaida depression and Lake Eyasi. It is the south-eastern extension of the great *G. swynnertoni* belt of Shinyanga and eastern Mwanza. On the east of Ufiome and coming westward, north of that mountain, on a broad front to the foot of the Great Rift Scarp, is a fly belt—that of Mbugwe–Babati—consisting of *G. morsitans* and *G. pallidipes* mixed with some *G. swynnertoni*. Further east in Masailand, only *G. swynnertoni* occurs. The belt then swings off to the Moshi District in the east and towards Kibaya in the south. The *morsitans–pallidipes* belt of Babati–

Mbugwe sends a narrow strip of these two species northward between Lake Manyara and the Scarp, and this, half-way up the lake, gives way to a strip of *G. pallidipes* with some *G. swynnertoni*. This again, north of the lake, broadens and joins with the Moshi-ward belt of *G. swynnertoni* referred to already, which passes east south of Arusha. Most of the infested country is occupied also by *G. pallidipes*, but this does not apply as yet to the *morsitans* belts of Kikore and the Bubu, referred to below. In the south of the district, the *morsitans* belt of Kondoa (of which a full account is given on p. 424 below) finds its northern limit astride of the Bubu river from Bereku to Masagoloda. Some of the above may be followed in maps 1, 5, and 6.

The effect of exceptional seasons may be seen in the fact that flies of the low-lying parts of the Mbulu belts showed the reduction in numbers that the concluding burst of rain of the season 1929–30 inflicted on those of Kikore.

Within the general fly areas referred to above, there are in Mbulu six distinct " fly situations." The problem of the western Barabaig country is dealt with under the heading " defence against fly advances " (p. 435 below). That of Kiratu–Oldeani—the opening up of large areas north of Mbulu that have so far been barred off by the flies—is dealt with on p. 398 below. The advance northward of the West Kondoa (Bubu) fly belt would seem, at Masagoloda at any rate, to have reached the utmost limit to which it can readily advance. Whether it can swing to the north-east to Pienaar's heights is more doubtful. A flight which I made over this area in 1929 suggested a danger of this. Not dissimilar is the position of the Wambugwe, under the Rift Wall south of Lake Manyara, the only Bantu tribe in the district. Some small clearing has been done and not a great deal more appears necessary. There remains to be discussed here three situations only—that between Ndereda and Babati, that south of Mount Ufiome, and the possibilities on the Yaida river.

(b) The Ndereda-Babati line.

A band of highly attractive hill country, largely open grass country covered in parts with low, very open, savanna wooding of *Protea*, *Faurea*, *Terminalia torulosa*, and their associates, runs across between the Rift Scarp just north of Ndereda to Mount Ufiome. It falls off to the north in a scarp of its own. Below this strip, to the north, is the Mbugwe fly belt proper of *G. morsitans* and *G. pallidipes*, with some *G. swynnertoni*. A group of coffee plantations, owned mostly by Greeks, lies in its midst. Along the high hill band stretches a line of farms belonging to other Europeans, who are also planting coffee. The two farms next the Rift Wall are more heavily bushed than the others, and Farm 2910 with the land adjoining it on the east appears still to be rather a danger point.

The surge of the tsetse population on the north, against the foot of the farmed hill scarp carries constantly a number of flies over the top and these in turn threaten the lower country beyond, belonging to the natives (here Wambulu and Wafiome), that adjoins the hills to the north.

The settlers here agreed to a scheme whereby they and the Government should clear a band through the farms—on the southern side of the farms to work in with the native clearing to be mentioned—and the tribes were to make their native clearing along the south of the farms. This last was early carried out and the clearing along the farms is being completed by instalments. Stumping is being adopted here owing to the free and speedy regeneration of the Proteas. The work has been under the direction of Gordon-Russell.

To my mind the main danger, apart from flies carried on lorries coming south

from Arusha through the Mbugwe–Babati belt, is from *G. pallidipes*. A "deflying post" has been in existence for many years near Babati to minimise the danger from lorries; but that *G. pallidipes* is beginning to filter through is shown by the capture of two examples near Kikore, where, despite Nash's and Lloyd's intensive work over five years, this fly was never before found. There is also the remote danger of *G. morsitans* working in from the eastern flank past Mount Singi that is referred to below in the discussion on Ufiome. The scheme described is the right one and the only addition suggested is one of which plans were submitted to the Administration long ago—a "Rhodesian" deflying house on the road instead of the inadequate, and inadequately supervised, native defliers.

(c) The position in Ufiome.

The position here is exceptionally serious. "The Wafiome (properly Goroa) are a Hamitic tribe practically identical with the Wambulu. . . . They are both agricultural and pastoral. . . . Their country is being encroached on by fly and cannot support them, and they are invading the country of the Barabaig. Numbers of Wafiome migrated to Kondoa–Irangi. . . . The Wafiome number 14,000, owning 37,000 cattle and 22,000 small stock" (Bagshawe). The latest figure of emigration given is 9,000, mostly to Kondoa–Irangi, out of an original total said to have been 15,000. It is suggested that the tsetse is not the sole cause, but it certainly is an important one. It is the vicious circle which we saw at the first in Shinyanga. As people leave the tsetse come in, as the tsetses come in more people leave. The principal fly in question is *G. morsitans*.

It seemed to me some years ago that the remedy lay in the cutting of the Ufiome–Kikore fly belt—which is not wide—into blocks, on the Shinyanga model, and a subsequent attack on these blocks. The "barriers" between the blocks would be cleared by the tribe—and settled; and the blocks would be attacked by the Tsetse Research Department, if funds should be available. I suggested, first, that when our scientific investigation was over, there should be constructed * a broad barrier disconnecting the permanent fly of the scarp-side that bounds the area on the west (the scarp-side in which Nash carried out his parasite measures, discussed on p. 241 above †), from the low-lying land between it and the great north and south mbugas (*see* maps 1 and 4 and p. 399 below) which here divides *G. morsitans* (in the west) from *G. swynnertoni* (in Masailand, in the east). Secondly, I contemplated the establishment of a settled clearing along the Kikore river (*see* map 4) which would be essential to protect the Kikore–Galapo block from re-infestation from the south. Further subdivision, further to the north, would be made later on. The low-lying blocks (east of the road) would, I expected, nearly clear themselves of fly in any future heavy burst of rains, as happened in 1929–30. A very little special work quickly carried out then and after a special fly survey, would probably be finally effective. Without relying on this, organised grass burning seemed promising and, since that date, not burning at all has proved itself and would, it is felt, be applicable. Work was proposed also against the permanently entrenched flies of the scarp-side, the latter covered with miombo and containing serried rows of the most magnificent breeding-places. A little special clearing was considered likely to be useful here, but it was proposed meantime to see what could be done with log-traps (pl. 10, fig. 1). This work would be definitely experimental.

* It was proposed that this should be constructed along the road shown in map 4.

† This is coloured pale green on map 1.

Gordon-Russell, with tribal labour, duly carried out the north-south clearing from Hanara near Galapo to Kikore to separate the scarp from the flat-lands. Ring-barking, not felling, was used, as it was expected that the Central Province settlement, on the Kikore river, would take some years to complete. Actually it is now about to be undertaken vigorously. Whether the work will be completed in time to prevent the emigration of the last few thousand of the tribe is not known, but doubtless, when this fly situation and any other grievances are righted, they would drift back to a chief whom they liked.

(d) The Yaida problem.

The Yaida river flows from the Nou Forest Reserve on the mountains south of Mbulu, westward down the mountain side, across a broad shelf, and down a scarp in the form of a waterfall, into the great Yaida—or "Hohenlohe"—depression. The eastern strip of the long north-to-south shelf referred to is occupied and grazed closely by Wambulu. Its western strip is annually, and mainly seasonally, invaded by *G. swynnertoni* from the dense infestation of the depression. On the Yaida there are two farms, one above the waterfall belonging to Dr. Trautmann, an ex-German Veterinary Research man; and one below it to Herr Michatz, an engineer. Dr. Trautmann is doing fine work for the discovery (apparently already most promising) of a cheap cure for trypanosomiasis in cattle. He was allocated the farm before the Oldeani settlement was opened. It was an unlucky allotment, as it is of little use for his purpose of coffee-growing and, in particular, it has had the effect of excluding the native cattle-owners from waters which they need very urgently. I found that it was proposed to cut corridors for the cattle round "Yaida Farm" to a narrow rocky space between it and the top of the waterfall, to enable the natives to water without trampling out the farm, but my recommendation was—land for Trautmann elsewhere and then let the natives use the water, instead of wasting money on clearing. For it seemed if the latter were made at all, that it would be better to locate it further south to divide the infested land of the Barabaig from the seasonally infested shelf south and north in Yaida. For, going over the ground, it had appeared that here was a case in which the incursion of the flies was in the main seasonal, the bush interspersion not being of a type to carry them all the year round excepting at limited spots which could be cleared. Further, if these were cleared and if a band of clearing were to run north and south along the edge of the scarp, and were settled, the bush between would fall into the lap of the natives for their use all the year round.

The conditions on the shelf are as follows according to Dr. Trautmann:—elevation 6,300 feet; windy; mean general temperature 18°–28° Celsius, for a few days each year 30°–32°, lowest 4·0°. Flies are seen at Dr. Trautmann's homestead (near the edge of the native settlements) only in April, and nagana breaks out chiefly between April and July. The flies almost evacuate the shelf or terrace in the dry season—one had been seen by Michatz' native road-party, working at the top of the Yaida Scarp, on the day that I was there (13th July), and the native cattle had grazed the grass for a long way westward towards the scarp. They are put in when the rains finish and the tsetses become "moja-moja" ("one-one").

There are more tsetses in the rains; and, during the great rains of 1929–30 and for most of the dry season after, there were very large numbers on the shelf. Here we perhaps see the obverse of the medal that shows on its other side the great destruction of tsetse in the flats at Kikore in those rains.

On the Yaida, it is probable that the flies (i) partly moved to the top away from the trouble below, and (ii) found the " shelf " more favourable to them than usual. " It seemed that the practical evacuation of the shelf each normal year by the flies (the extent of which evacuation to north and south should be ascertained) will be due (i) to the relatively open nature of the bush, without many thickets or glades, (ii) to the cold of the dry season at 6,000 feet. The composition of the bush as I saw it was mixed—but *C. Schimperi*, *Combretum* spp. including much *C. Zeyheri*, and *Acacia* (perhaps especially *stenocarpa* and *Benthamii*) were on the whole dominant and about equally so. *Combretum* is difficult to kill, *Acacia* is easily killed by ' slicing ' [fig. 27, 5] and *Commiphora* by termite-admission " (fig. 27, 3, and fig. 28) (Swynnerton, 1934).

Whether the scheme would entail more work than it was worth, whether there were better schemes to occupy the energies of the local natives, whether a mere modification of the bush on the shelf, perhaps with a very small barrier, would not suffice, and all other details, could only be found out by survey. Findlay has therefore been instructed to investigate the position and all its possibilities most thoroughly, preferably as part of a survey which shall bring up to date Gordon-Russell's surveys from the Singida border right up to Oldeani, inside this *swynnertoni–pallidipes* fly belt that occupies all western Mbulu. Findlay's survey would be followed by a complete entomological investigation of what may prove a most interesting situation.

(e) Two general considerations.

A general difference between Mbulu and the country of Usukuma in the Lake Province is that fewer natives are in most places available in Mbulu for the purpose of tsetse control, and one tribe at least, the Barabaig, will not do manual labour. But, for the Wambulu (or Erokh), at least, as for the Wasukuma, this tribe being fairly numerous and very willing to reclaim, the wise course is to lay down a far-sighted scheme as a framework for future measures, and to fill it in little by little. Hand to mouth work can only lead to wastage of money and labour, and trench-warfare advance by the mere swelling of population can only lead to an extension of erosion.

(f) Work done by the Tsetse Research Department in Mbulu in 1934.

The following work was done by Findlay in Mbulu in 1934 :—

End August–Early September. Reconnaissance of Galapo.
Mid End September, 1934. Survey and clearing of S. Galapo barrier.
Early October, 1934. Yaida survey (beginning).
Early November, 1934. Reconnaissance of Basotu, Ndereda.
November 30th, 1934. First general report on Mbulu fly situation.
Early December, 1934. Survey and demarcation of N. Galapo barrier.
Mid-December, 1934. Reconnaissance of Mbugwe.

11.—THE SCHEME FOR OPENING UP THE GREATER MBUGA SYSTEMS.

(a) The general scheme.

The areas in question may be classified as follows :—

(i) large pieces of country in which cattle cannot be grazed or used, not because the ground is infested, but because it is cut off from the nearest cattle-area by a band of tsetse-infested bush which cannot be crossed without disaster;

(ii) other areas which are only infested seasonally, the combinations of vegetation within them being adequate for the fly concerned only at one time of year;

(iii) a further category of country which does not contain the vegetation-concurrence the fly requires for existence, but which, nevertheless, is infested all the time, solely through the fact that suitable tsetse wooding adjoins it and the flies are all the time wandering in.

Under the first heading come some great mbugas and mbuga-systems of more or less open grass-country. These are mainly found in the thorn-bush areas (*see* pp. 385–399 below). Under heading (iii) may be included great parts of the mbuga systems (heading (i)) which are clothed with woods that consist mainly of the gall-acacias and are infested with tsetse only for the reason just given. Category (ii) is somewhat apart and is dealt with in greater detail elsewhere (*see* p. 260 above).

To make country in category (i) available for grazing it is only necessary to connect it with fly-free cattle-country by means of a cleared corridor of adequate width and to provide waters if these are lacking. To make country in categories (ii) and (iii) available it is necessary to make a clearing of adequate width and completeness round its periphery in order to separate the wooding that occupies its remainder from the fly bush proper outside and so to prevent infestation.

It is part of our programme to search for and plan for the utilisation of all such areas as come into the above three categories and can be utilised. Several thousand square miles might ultimately be developed by these means. The following will indicate what has proved possible already.

(b) The part of the Huruhuru system which lies in Shinyanga, Lake Province.

(maps 2 and 3.)

(i) *The general position.*

Lying between the conspicuous bush-covered hills of Buhungukira in the Kwimba district, on the north, and the thorn-bush area of Nindo and Old Shinyanga on the south and south-east, there is a great plain of, probably, 500 square miles. Different parts of it have different " mbuga " names and the name " Huruhuru " strictly applies only to the corner next to Old Shinyanga.

Many years ago the great plain was nearly all grazed, and when we began our work there was still a safe, broadly open strip by which the cattle of the chiefdom of Nera in Kwimba reached the waters and grazing of Mwantimanya. But the invasion of the Shinyanga thorn-bush by tsetse from 20 to 25 years ago led to the infestation and disuse of the greater part of the plain. The infestation was extending even to the parts referred to above as fly free, as for instance between Mwantimanya and Bukandi.

Part of this infestation is permanent. There are " islands," large and small, in the plain, the wooding of which is favourable, in the north-west to *G. morsitans*, with an overlap of *G. swynnertoni*, in the middle and south to the last-named fly only. But in the plain generally, in addition to large open spaces, there are extensive woods of gall-acacia which would normally be inhospitable to either fly but which owe their infestation to contact with the fly bush proper, of which a broad band also separates the plain from the great cattle-keeping areas of Shinyanga. It is only the south of the plain and the problem of relieving by its use the over-grazed areas of Shinyanga which are dealt with

here. Buhungukira, on the other side, has been dealt with in practice, and is treated here as a separate problem (*see* p. 370).

(ii) *The objects of the work.*

The tribe had attempted to make a corridor in 1929, just before we came back to Shinyanga, but, after some very imperfect clearing, had dropped it. It was apparently not realised then that the plains were infested with tsetse. The objects of our work have been :—

(α) to carry out the surveys, which were obviously required.

There were carried out, first, a general plane-table and fly survey by Findlay of the margins of the mbuga for a number of miles in, secondly, more extended surveys by Napier-Bax.

(β) to carry a corridor to the plains, which owing to their alluvial nature, were likely to stand grazing of great, but regulated numbers of cattle and also not to erode readily, and thus to relieve the disastrously over-grazed and rapidly eroding areas of east Shinyanga, success in our objective being a foregone conclusion;

(γ) to separate adequately the very extensive gall-acacia wooding of the plains from the fly bush proper wherever it came into contact with it.

Findlay's instructions were to work round the mbuga system, first south from the Mwanakoba mbuga inclusive (*see* map 2), then round the west and the north. He was to decide on the best route for the clearing to take and calculate between point and point, right round, how many acres of gall-acacia would have to be cleared to produce a continuous open strip up to a mile in width round the mbuga area. The presence of "fly" and "fly-free" areas was to be noted, as well as the grass and the waters. Findlay found that generally speaking, "scattered flies were found all through the gall-acacia areas. In some cases flies were taken right out in the open mbugas but in no single instance were they more than a quarter of a mile from either trees (gall-acacias), game or man."

The flies scattered through the mbuga woodlands were certainly dependent on the game, just as they would have become dependent instead on the cattle had the latter been introduced. The game totals seen were : eland 48, roan 21, topi 581, wildebeest 4, giraffe 33, zebra 60, impala 8, Thompson's gazelle 120, reedbuck 27, Defassa waterbuck 3, ostrich 26, wart-hog 2 and lion 1. This gives an idea of the very sparse population of large herbivora that inhabited this vast plain and of the boon to the flies and their probable inordinate increase if the many thousands of cattle which are likely to graze these plains had been introduced without the prior precaution of a barrier clearing.

In actual heavy rains there was no dearth of water. In the late dry season water was only obtainable at six points in the whole plain and at only four of these was it possible to water great numbers of cattle. These four permanent waters were at Bubiki (road junction north of Mwanakoba mbuga), Salawe, Ngongho (where cattle using the Mwantimanya grazing were watering), and a lake which forms a link in the seasonally flowing Isanga river that connects the Ngongho Pools with Lake Victoria. Thus, even if the flies could be excluded from the wooding of the system, new waters would have to be provided.

Detail was duly provided by Findlay as to the various areas of contact between gall-acacia wooding and fly bush and the location and amount of the clearing that would be necessary to break each of the contacts.

(iii) *The clearings carried out.*

The following is quoted from a report (dated 18th February, 1934) by Napier-Bax, Senior Field Experiment Officer, to whom, and to Vicars-Harris in Napier-Bax's absence on leave, have been due most of the planning of detail and (with men under them) all the execution of this very important work :—

(α) *The year* 1932.

"This year was devoted to making the Beda corridor which had been started and which through the pause of some years . . . showed much regeneration.

"3,560 men worked their 10 days on this long clearing. It measured 10·2 miles in length and 1,200 yards in breadth over the greater part of its length, but in the last three miles it widened to a breadth of 1,400 yards.

"The number of tsetse present in the newly-felled corridor and in the ilula belts springing from the main fly bush and stretching far out into the mbuga prevented our putting cattle into the Huruhuru that year, although the short rains filled Stiebel's tank."

(β) *The year* 1933.

"The corridor completed, the 1933 season was directed to 'cleaning up' the eastern end of the Huruhuru and the provision of more water. The open mbugas were 'tidied up,' Sayu was freed of its fly-bush elements and the ilula (gall-acacia) was isolated from the main fly bush as far west as Half Way Camp [the westernmost point on map 2] and northwards up to the Seke road over a total distance of some 18 miles. In addition, a tank at Sayu was excavated. It took 3,530 men to complete this programme, approximately the same number as the year before."

The barrier against tsetse that was thus interposed between the gall-acacia woods and the fly bush took the intended form of a series of clearings round the perimeter, advantage being taken of every patch of open country which would make it possible to reduce the area of the actual clearing. In preparation for the coming of cattle, kraals were built to accommodate well over 1,000 head —some at Sayu, some in the mbuga north-west of Mwalukwa (*see* map 2) and some near the entrance of the Beda corridor.

(γ) *The year* 1934.

"In the mbuga itself the Huruhuru reclamation programme for 1934 was confined to consolidation rather than to extension. Here Butuyu island was cleared and the remaining bush on Sayu felled while the clearings isolating the gall-acacia from Half Way Camp to the Seke road [old Mwanza road] were broadened. . . . However, the break-through from the south was pushed forward with energy and in particular a southern arm of the mbuga was extended. . . . This extension will in due course form part of the southern break-through. Altogether 5,524 men worked their ten days on the scheme, some 2,000 more than in either of the two preceding years."

At the end of the clearing in 1934 the gall-acacia woods were at no point in contact with fly bush from the Mwanakoba mbuga in the north round to Nindo, and the width of the barrier was everywhere good.

(iv) *The provision of water.*

(α) *The year* 1931.

In 1931 a bore-hole was put down by the Geological Survey Department in the south-eastern corner of the plains. It struck water but in small quantity

and deep. Of several bore-holes put down since in the northern part of the plains most have been failures, one a success. In the same year an earth-tank —a large oblong hole in the ground—was dug by the Administration in the eastern edge of the south-eastern corner of the plain on the instructions of Mr. H. C. Stiebel, then Provincial Commissioner. Though a recognised form of storing water in deep stiff clay and recommended by the Geological Survey Department, it was a pioneer undertaking and an experiment under the local conditions; for it broke through the few overlying feet of black alluvial clay, which we knew would hold water, deep into the underlying, broken-looking white "cement." In its first season it failed to hold water. By the second season the cracks had sealed themselves and it held water splendidly. Many such tanks are now being dug in the same formation—here and in Maswa and Kwimba—and there can be no doubt that they will be the means of enabling great areas to be grazed.

(β) *The year* 1932.

"A series of test-pits were put down in the Huruhuru by ourselves with the aid of a small gang of tribal labour supplied for the purpose. The black clay was found everywhere to peter out at a depth of eight or nine feet."

(γ) *The year* 1933.

Under the supervision and at the expense of our department, Stiebel's tank having now proved itself fully, a really large earth-tank was made at Sayu, further out in the Huruhuru mbuga, to hold 750,000 gallons of water. This is shown in fig. 1 of pl. 10. The following is a further extract from Napier-Bax's report :—

> "The poor rains of late 1933 were reflected in the disappointing manner in which the tanks (Sayu and Stiebel's) filled, for during these short rains they were never full to the brim. . . .
>
> "During the long rains of 1934 Stiebel's tank filled to capacity and Sayu also filled to the brim. Towards the end of the rains all the cattle in the mbuga were concentrated on Sayu (as well as hundreds of tribal labourers) as it was desired to reserve Stiebel's tank for later gangs of tribal labourers, settlers and a few local herds. . . . Sayu finished on June 18th and the tribal cattle were evacuated. Stiebel's tank held water excellently and did not finally give out until well into September."

(δ) *The year* 1934.

"The Sayu tank was developed [further] and new tanks were begun at Half Way Camp, Seke and Butuyu. The total tank capacity is now in the region of 3,000,000 gallons. . . . A southern arm of the mbuga was extended to open up to cattle some large pools on the Ningwha. At the end of October there was sufficient water in Sayu tank (it overflowed before November) to invite 2,000 head of cattle from the eastern sultanates. The Seke tank also half filled in early November" (Napier-Bax).

The great number of cattle that were grazing in the area by the end of December (25,000, see below) were a testimony to the abundance of water provided. At one time 10,000 head of cattle were being watered daily at Sayu tank alone. A section of the Sayu tank is shown in pl. 16, fig. 1.

(v) *The results so far obtained.*

The breaking of the contact right along has had the expected result of practically freeing the gall-acacias from flies. The "island" of Sayu, lying

in the south-east corner, remained a trouble, being too near the fly bush of the Nindo section on the one hand and that of Block 11 on the other, flies being carried into it also in numbers on men travelling on a path from Nindo. But by 1934 it had been cut out completely.

Leading to the south-eastern plain area, part naturally open country, part gall-acacia but freed of fly as described above, the tribe now possesses an open corridor from 1,200 to 1,400 yards wide. This is not completely fly-proof, for flies come into it on native paths and, reaching the road in the centre, tend to hang about there, but we find that the passage of two fly boys with a screen ahead of any mob of cattle passing through " sweeps " up these odd flies most effectively and this safeguard is regularly practised. The flies come from Block 10 and the 200 yards' fringe of Block 10 that abuts on the corridor is being kept unburned for the sake of the old grass mat which is apparently deterrent to the flies and for the upgrowth of thicket. Judging from analogy elsewhere in the area, the change that will come about in this strip will at least stop the flies from coming much into contact with the edge of the clearing and wandering into it uncarried. In any case the present width of corridor is temporary. The whole strip south of it is already responding to our measures against the tsetse contained in it and, when its reclamation is complete, the corridor will be not 1,200 yards but fully three miles in width.

At the end of 1933, the second year devoted to the scheme, it was possible to invite cattle to graze in the mbuga. Moggridge, under whose control the cattle and grazing were first placed and who was housed out at Beda, organised in great detail a routine for the reception of the cattle at kraals at the eastern end of the corridor, their passage through the corridor and their reception in the Huruhuru. An African assistant was stationed at the main kraal (erected by the Department), and it was to be his care to see that the herds were not grazed in too close proximity to the fly bush. Kraals were specially built for the accommodation of the incomers in the Huruhuru mbuga proper. 1,000 head of cattle had been promised by the tribe as an " experimental herd," but when it came to despatching them their confidence failed and, professing fear of a poisonous plant, they suggested that the Department should lead the way with cattle of its own.

*The first days of 1934 saw the first herd in the mbuga, for on January 2nd the Department despatched 100 head of its own cattle to pave the way for the Chiefs. The sultanate of Seke, however, though they had been foremost in protesting their fears of the poisonous plant, were among the first to exploit the newly-opened mbuga to their advantage, for about 1,200 head which had arrived from the north were observed from Sayu during January. During the first days of February, as the natives gained confidence, small mobs of cattle began to arrive through the Beda corridor and by March 21st there were 557 cattle housed in our Sayu kraals. Moggridge reported an almost immediate improvement in the condition of the cattle following their arrival. This is not astonishing considering the abundance of green grass and water and the fact that in spite of their wretched condition much of the stock sent was young.

The herds of " screws " sent by some chiefs were only explicable on the grounds that they considered despatch to the Huruhuru tantamount to sentence of death, and were determined to sacrifice only those that they thought would die in any case. But they did not die. Time and again the Stock Inspector and the Chiefs visiting the herds all expressed their amazement at the rapid

* **Extracted from the report by Napier-Bax.**

improvement. Our own slaughter herd that had been out longest in the mbuga were specially remarkable for their magnificent condition.

By May there were 2,149 cattle housed in the Sayu kraals, made up as follows :—

Tsetse Department	214
Kizumbi	290
Chief Makwaya (Grazing experiment)	100
Ibadakuli School	170
Usiha Chiefdom	1,090
Mwadui „	259
Sayu settlers	17
Total	2,140

The figure does not include the Seke cattle. No further attempt was made to count them, yet they were undoubtedly present in large numbers towards the north end of the mbuga and at a hazard might at least be put at 2,000. On June 18th the water in Sayu tank having become very low, all tribal cattle were evacuated and there only remained our own and some belonging to the local mwanangwas [village headmen]. These watered at Stiebel's tank until it dried up in September when they watered at Beda, but they grazed and slept in the mbuga as before. This practice continued until, with the advent of the short rains, there was once more water available at Sayu. But in addition to these small numbers the northern areas continued to be grazed by Seke cattle throughout the winter. On the road from Seke tank to Butuyu during the dry season it was by no means uncommon to see 20 or more herds of cattle of from 20 to 100 head. How many more were hidden in the bush it is impossible to say. But the state of the grass and the numerous cattle tracks indicated the heavy grazing that was taking place.

The position at the end of 1934 was as follows :—At the end of October there was sufficient water in Sayu tank (it overflowed before November) to invite 2,000 head of cattle from the eastern sultanates.. The response [from the east] was slow, but local cattle owners (mostly from Seke), who have settled at Sayu, brought their herds in at once. Indeed there had been great difficulty in keeping these people out and convincing them that during the dry season only a limited number could water at Beda. The new Seke tank also half filled in early November, but even a month before this Seke cattle appeared in their hundreds in the neighbourhood. On the road from Seke tank to Butuyu, herd after herd is passed and Butuyu itself has become a cattle centre at least as important as Sayu. The great boma (enclosure) built by tribal labour on the crest of the hill is full, while numerous smaller bomas each holding their quota of cattle have been built in the vicinity. . . . But this is not all the tale, for Seke men have built temporary kraals in the gall-acacia to the south and west of Butuyu. As at the beginning of the year, their herds are once again sighted at Sayu. There can be no doubt that the mbuga system will be used by a really large number of cattle this year.

With the filling of the tanks by good rains at the end of October 1934 it became possible once again to invite in cattle. That they entered freely is shown by table 58 on p. 391.

It will be noticed that cattle from " other districts " have been a quarter of the total. . . . This shows great lack of initiative on the part of the Shinyanga cattle owners who are permitting the fruits of their exertions to be reaped by others.

TABLE 58.

The number of cattle utilising the Huruhuru mbugas, newly cleared of flies, in November–December 1934.

Date	Shinyanga District	Other Districts	Total on the date stated
1934.			
24th Nov.	11,594 (from Seke sult. alone, 10,452)	3,697	15,291
1st Dec.	16,201 („ „ 13,863)	5,914	22,115
8th Dec.	19,077 („ „ 15,490)	6,466	25,543

The most significant feature of the above figures is that the Seke cattle formed nearly the whole contribution of Shinyanga district at the end of the last year, while even to-day they form about 75%. Further, Chief Makwaya of Usiha has 1,325 of his personal cattle in the mbuga (sent as a gesture to encourage others). If these and the Seke cattle are excluded, we find that 1,803 is the contribution from the eastern Shinyanga district! Indeed at present only two sultanates besides Seke are represented (Usiha and Shinyanga). The Mondo people, notorious for the reckless and wholesale manner in which they have been grazing their cattle in fly bush, have none at all in the mbuga at present and never at any time had as many as 2,000. Usiha itself has been disgracefully backward in sending cattle and also has never exceeded the 2,000 mark. Not a single head has come from the remaining contiguous sultanate of Mwadui.

The sultanates which contributed most to the work are using it least, while cattle from other districts—districts which have taken no part at all in its reclamation—are present in large numbers. At the same time shortage of grazing has been as severe as ever in the Shinyanga district, and we have had recent examples of wholesale invasion of fly bush by starving herds with the resulting penalty of heavy mortality from trypanosomiasis. As already mentioned (*see* p. 291 above) cattle from Mwadui and Mondo—the people who made the corridor—invaded our heavily infested Block 9 by the many thousand, ruined our game-experiment and died in numbers.

The reason why Seke has such a good record and the other sultanates such a poor one is not far to seek. Seke sultanate borders the northern edge of the area and it is consequently easy for the Seke men to graze their herds there, in fact they have long utilised the strip adjacent to their homes which has been fly-free for many years. The reclaimed area was merely an enormous extension of country with which they were already familiar.

But lack of familiarity and fear can no longer be regarded as a legitimate excuse for the other sultanates, however great the part they once played. In the course of the last three years thousands of the common people have themselves seen the area; the Department has time and time again organised lorry trips for chiefs and mtwalis to the mbuga; the men have been told the successful results with the experimental cattle of last year, and many of them saw the cattle themselves and expressed amazement at the spectacular improvement in their condition; and if further proof is needed it is generally known that Nera and Seke have for years sent mobs of cattle to the limited section of the north of the system that was fly-free already. Finally there are the very large numbers of cattle grazing successfully there during the last few months.

It is rather the difficulty of maintaining the herds away from home, especially the small herds of 20 beasts or so. In the home pastures a single herdsman is

sufficient and is probably a child. But if cattle are to be sent thirty or more miles away a youth or man has to go and the child is still needed to herd the cows, required (very properly) for milk, at home. Thus the family man-power is depleted. At the end of the dry season too there is generally a dearth of food, and while it may be easy for the family to scrape a hand-to-mouth existence at home till the new crops come in it is much more difficult to gather a month's supply for the distant herdsman, while the porterage of fresh supplies of food is also a consideration (Napier-Bax).

It is hoped to overcome this difficulty by employing for each village herdsmen, perhaps paid by the tribe, approved by the owners of the cattle.

(vi) *A grazing experiment.*

This experiment was carried out in co-operation with and according to the specification of Mr. R. R. Staples, the Pasture Research Officer of the Veterinary Department. A 50-acre plot was demarcated in the Huruhuru by Moggridge for the accommodation of the experimental herd during the wet season and a kraal was erected and Moggridge took charge of the experiment. The plot was grazed as follows :—

April 12th to April 25th . . .	100 head (14 days)
May 10th to June 17th . . .	50 ,, (38 days).

Thus an average of 50 head were grazed on the plot for a period of 66 days. At the close of the experiment the animals were in excellent condition. A complementary plot (for dry-season grazing) had been established by Staples at Negezi in the over-grazed areas of the east, to which our mbuga grazing (to be used in the rains) was intended to give rest and relief. Staples on visiting us was able to report that " the area, when compared with the surrounding almost completely bare land, affords a most striking demonstration : the condition of the stock was good " (with the exception of two fly-struck animals) " and there is a sufficient grass cover to prevent serious erosion with the advent of the rains. The more valuable perennial grasses appear to have increased markedly and an even greater improvement can be expected if the pasture is rested again during the coming wet season. Regarding the running of the trial for the coming season, it was arranged that the herd should be put back on to the mbuga pasture as soon as water is available in the dam " (report by Staples dated 7th February, 1934). Our mbuga pasture had stood up to its grazing well, despite the facts (α) that the land included much hard-pan with poor grass, (β) that the failure of the rain largely inhibited the grass growth in the better portions of the plot, and (γ) that, through inability to fence, the area had been subject to strong incursion of native stock from outside, though the 50 experimental animals had been grazed within it.

The experiment was therefore altogether a valuable contribution to the " rotational grazing " question described below.

(vii) *The future of the Huruhuru system.*

Discussions took place between Mr. Staples, the Administrative Officer (Mr. R. W. Varian), and ourselves, on the future grazing policy of the Huruhuru system. That the area should be used as rainy-season grazing, for the rest and relief of the over-grazed, eroded eastern area, was stressed and generally agreed to, at least till adequate dry-season waters could be provided. Staples visualised, however, a sort of communal grazing park to be opened for cattle at the beginning of the rains, and the transfer thereto from the adjacent cultivation

steppes of all the cattle with the exception of young stock and cows. Settlement was to be excluded. We, on the other hand, maintained that, without prejudice to the use of the area as a wet-season reserve, it was of primary importance that encouragement should be given to permanent settlers to come with their cattle and make their homes there. Grazing without settlement would result in regeneration of bush on the high-lying pieces of ground on the margins, where we had cleared it, and the consequent necessary slashing back of this growth from time to time to prevent re-infestation by tsetse. The areas to be opened were so huge that conflict between the interests of settlers and graziers from outside was unlikely, at least under proper regulation. It was suggested in reply that as these areas were being opened by communal effort, the latter could also be used to slash regeneration in future and keep the bush low. We for our part believed that an adequate strip of settlement between the fly bush and pasture was the safest insurance for the future. Admitting settlement, Staples urged that, just as the cattle from the over-grazed areas are to come into the mbugas in the rains, so the cattle of the permanent settlers there should evacuate theirs in the dry season and send them to the rested pastures to the east and south; leaving only the milking cows. Thus the rotation principle would be maintained. We replied that the main objection was that the system would form a deterrent to settlement round the mbugas, to which the reply was that the water shortage in the dry season would form an adequate excuse. But this shortage is being annually made less.

The comments of the District Officer were that we would have difficulty in the first year or two in accustoming the native to parting from his cattle in the rains; that the chiefs at the moment preferred the idea of using the mbugas in the drought; but that they certainly could be converted. He foresaw trouble as regards herding, as a man could not leave his cultivation in the rains to be with his cattle elsewhere. Paid herdsmen would be necessary, but this was probably not impracticable.

The utility of using the plains as a relief for the over-grazed areas has, it may be said, been well demonstrated by the capacity for recovery shown by such an area at Negezi, formerly completely over-grazed, that has been held free of cattle; and it is anticipated that the whole area of nearly 400 square miles that lies in the Huruhuru system in Shinyanga district alone will, when the remainder is opened, take all the male stock it is proposed to evacuate from elsewhere during six months in the year.

The general upshot is that the mbuga system, at least for some years to come, is to be regarded as a wet-season ground for the existent settlements east and south—the male stock being brought in about Christmas and evacuated again about June; that settlement round the perimeter of the plains will be encouraged; that an increasing number of earth-tanks will be provided each year till the plains are completely equipped; and that a herding system will be tactfully organised which should break down the fears of the cattle-owners. The present cordial and profitable co-operation in the matter between the Administration, the Veterinary Department and ourselves has proved of the greatest value.

(viii) *Summary.*

" That part of the Huruhuru series of mbugas that lies in Shinyanga District is about four hundred square miles in extent. It is largely covered with ilula [gall-acacia] bush and up to recently was almost wholly infested by fly. There are areas, however, amounting perhaps to 70 square miles, that probably

have always been free of fly and have regularly been grazed, often during the rains (when water for stock was plentiful).

" Since 1932 some 12,500 Shinyanga tribesmen have worked their 10 days on the reclamation of the infested area (planning, marking out, tools, supervision, meat, etc., being supplied by the Tsetse Department). This includes labour employed on completing a 15-mile cattle corridor through fly bush from the east, isolating the ilula bush of the mbuga, clearing two fly-infested ' islands ' of bush, providing 3,000,000 gallons of water-storage in earth-tanks, augmenting this supply by opening a bay to some pools on a river, construction of cattle kraals and the commencement of another cattle corridor to aid the southern sultanates. The result of these efforts is that well over a hundred square miles of new country * with adequate water for at least 6 months of a normal year is already available for the Shinyanga cattle.

" With the spade work done this area can now be trebled with comparatively little labour. In fact we have in sight provision of grazing for the whole male stock of Shinyanga during the whole rainy season when an acre of these rich pastures will carry a beast—as a special experiment has shown " (Napier-Bax, report).

(c) The Manonga mbuga system in south Shinyanga, stretching to the Manonga river.

(maps 2 and 3, and fig. 26.)

This mbuga system had been cut off from utilisation by cattle by a narrow but infested belt of gall-acacia on its east. Moggridge cut through this in 1933. It was at once utilised and many thousands of head of cattle have since been

FIG. 26.—Part of the mbuga system north of the Manonga river broken into by Moggridge.

grazing there. Moreover, an area of bush to the south of the corridor has become free of flies apparently owing to the preclusion of reinforcement by the barrier formed by the corridor.

* A very much larger figure than this has been rendered available at the time this paper goes to press.

(d) The Wida mbuga and the Dasina promontory in Maswa.

(map 3.)

The Wida mbuga was first reported to me and roughly mapped by Capt. M. S. Moore, V.C., then Reclamation Officer in the Department, now Game Ranger of the Serengeti. It is about 50 square miles in extent and Moore suggested that, in order to help to relieve the congestion of grazing in Mwagala, in Maswa, contiguous to it, a corridor might be cleared to the mbuga. This corridor was begun under Teare in 1928, and pushed through, but not to its full width. Then came the interruption in the sequence of the reclamation work referred to already elsewhere, and this scheme, amongst others, was shelved. It was even argued that there must be something wrong with the grass or the natives would have been using it already!

In 1934, co-operating with the Administration and tribe, we marked out the full limits of these two corridors afresh and the tribe, with our co-operation, carried them through to completion. Vicars-Harris did the surveys and Wheeler the supervision of work. The Administration have put in a first earth-tank on the model of ours in the Huruhuru, under our supervision, and it is proposed to add tanks yearly.

The result of these measures has been that many thousand cattle are now grazing the Wida mbuga.

The Dasina Promontory. This is a tongue of bush, several miles long and 3½ miles broad at its base, which extends out eastward between the densely-settled cultivation steppe of Luguru in Itilima to its north and the Wida mbuga and, at its end, turns a "nose" down into the mbuga towards the main fly bush on the Simiyu river to the south, over a mile away.

This tongue was cut off from the main bush *to the west* by the corridor, referred to above, that was carried into the Wida from Luguru. Its remnant is about five miles long and its area about nine square miles. It was investigated by Vicars-Harris in February of 1934, before the corridor was completed, and again in September, when the corridor had been carried to its final width of one and a half miles.

The bush is very large stink-bark (*Acacia usambarensis*) and *Commiphora Schimperi*, with little else, though gall-acacia strips occur. Thicket is practically absent, so that this element in the vegetation-concurrence that seems requisite for *G. swynnertoni* is wanting. The question has been "will the separation of this promontory from the main bush clear it of flies?"

When Vicars-Harris made his first reconnaissance the bush was full of game which grazed in the Wida at night and lay up in Dasina in the day. Large herds were seen of roan antelope, zebra, wildebeest, topi, etc., with two prides of lions of seven and four. Cattle were entering the island despite the presence of tsetse. On his second safari there was no evidence of cattle on the island and hardly any of game. On the first occasion four flies were encountered, but their presence was reported all through the south-western portion. On the second an occasional fly was taken, two together being found only at a minute patch of thicket—the only thicket he had been able to find in the island—near a dry water-pan. He suggested that the bush was unsuitable for the persistence of *G. swynnertoni*. "I do not believe," he concluded, "that the island will ever give trouble now that the Mwamwita clearing is clear and widened. Such small infestation as it may carry will probably be confined to a few odd flies brought in on herds of game from the Kimali bush or from the Simiyu." It will be seen that the cutting off of this "Dasina promontory" is probably

reproducing on a small scale exactly what occurred in the extensive gall-acacia wooding of the Huruhuru when we severed it from the source of its infestation, and also what happened south of Moggridge's corridor (para. (c), immediately above).

(e) The Ntukuza mbuga and similar small mbugas generally.

(map 3 (upper portion).)

This and all the country surrounding was investigated by myself in May of 1922. I wrote (p. 336) :

"At the Ntukuza mbuga, two miles broad by possibly twice as many in length, which we worked to get an idea of the position at these natural open spaces haunted by game, occasional flies were taken up to 500 yards out in the ilula-clumps (gall-acacia)—more or less connected by a few bushes and small clumps with the main bush containing fly—but none at all in the open, though we put up topis, zebra and roan antelopes, and at once worked along, men and bait-cattle, in their tracks. No puparia could be found at the water-hole, at which the game drank, in a small patch of *Acacia* that included one or two large and shady trees. In this mbuga there are four small herds of cattle, living safely, their owners state, and those I saw certainly looking well, in close contact with the game and much attacked sometimes by Tabanids. The game is regarded as coming out and living—and sleeping—in the mbuga to escape the attentions of the tsetse in the bush, and the tsetses are said not to follow them into the mbuga unless in ones and twos, as they 'fear the hot sun.' The game retires to the shade of the clumps in the heat of the day.

"From this and other evidence, I judge that the danger to cattle from game wandering on its pasture out of fly-infested bush will not be great, provided that the clumps of bush on the pasture are cleared or the cattle kept away from them.

"While at Ntukuza I was told of two fly-surrounded mbugas near the Duma, at one of which (Inyamageni, stated to be much smaller than Ntukuza) cattle, it was alleged, had been kept in safety for many years; while at the other (Magerani) small losses were always taking place. . . .

"Instances occur also elsewhere, in the territory, of fairly successful cattle-keeping in diminutive, fly-surrounded open spaces. Safe water, avoidance of too close approach to the bush and avoidance of much frequented paths and villages would seem to suffice; and it seems to follow from this also that the fly does not venture [far] uncarried into open country unless to conspicuous objects within a limited range." (Swynnerton, 1923.)

Since then further evidence has been obtained which enables us to say that cattle or game grazing in an mbuga within tsetse eye-shot of the bush are liable to attract hungry flies.

The flies in the country generally were hungry. Game then was scarce away from the mbuga.

Vicars-Harris and Potts re-investigated Ntukuza and its surroundings in February of 1934 in company with the District Officer with a view to deciding on the site of a corridor leading to it from the wide sleeping-sickness clearing on the Simiyu river, sixteen miles long, which in 1922 did not exist. They found that a line drawn east from the head of this clearing would only be three miles in length, the last mile of it passing through very open country. The islands of gall-acacia in the mbuga will need clearing as well. Game was more abundant and the flies were well fed. Wheeler has since carried out the detailed survey.

(f) The Wembere Plain.

(maps 1, and 3 (lower right-hand corner).)

This is an enormous plain measuring 3,500 square miles. It is bounded on the north by Shinyanga district and (to the north-east) Meatu in Maswa, by Mkalama and Singida districts on the south and south-east, by Tabora on the south-west and by Nzega on the west. Much of it is flooded in the rains, but it is for the most part good grass-country and a great deal of it is grazed already. A great area is completely open, but for many miles into most of its margins extend woods of *Acacia rovumae* and its associates, in addition to groves of the gall-acacias. Surrounding the plain, further back, on certainly half of its periphery, is extensive wooding of miombo well infested by *G. morsitans*. The *morsitans* infestation has in late years extended nearly to the plain in the Nzega district and is to-day rapidly advancing northward in Singida up the east side of the plain. As it advances in the miombo wooding on this side it also infests the *A. rovumae* wooding of the plain and it is probable that in the end only the open parts of the plain will remain available for grazing. On the north-west and north-east sides of the plain are infestations of *G. swynnertoni*, one of which, at least, is spreading (Ngurube, p. 379 above), and, working down the west side, may infest the entire periphery.

The open part of the plain in the north (between Nzega, Shinyanga and Mkalama) is very extensive. Access to it is still available from Ngurube (in N.E. Nzega), Shinyanga and the Sekenke section of Mkalama, but additional waters are needed to make permanently suitable the sections away from the dry-season pools of the Manonga river in the north and the Sekenke waters including Kenworthy. We regard the provision of this water as a scheme to be initiated when we next take stock of the whole position in this plain. The extension to the centre of the plain of the fly barrier now being cleared from Singida through Usule to the Wembere (*see* p. 434 below) will incidentally give Singida a corridor to the plain of which it has lost so much through this recent invasion by *G. morsitans*.

The reclamation of the infested portions of the Wembere and its full utilisation for stock is a matter to be borne in mind for the not very distant future.

(g) The Serengeti Plains.

(maps 1 and 7, and pls. 1, 2, and 4.)

These are mentioned because people have sometimes discussed the extension of our corridor method to the fly bush that lies between Maswa and Musoma and the Serengeti, with the idea of pouring out on these plains dense masses of Usukuma and Ikoma cattle. I mention this solely to express the strongest disagreement with this suggestion. We have in these plains, in potential existence, by far the finest, most celebrated and most visited National Park in the world. Having made some study of the American Parks, having visited the rightly famed Kruger Park in the Transvaal and seen the Serengeti as well and helped to feed its lions, I make the above statement with the very fullest conviction and add that no number of extra cattle for the Wasukuma, destroying this country as they have devoured their own, no *small* gold mines, no other form of development of which the area is capable, will make up to the world for the loss of the pleasure and interest to be gained from continuing to see, tame and at closest quarters, the old African fauna, antelopes in countless thousands, rhinoceros, and lions, for which these plains will give the opportunity when the

game generally, elsewhere, has gone, or to the Territory for the revenue it will literally " coin " in the future if a really great and wisely managed combination of Sanctuaries and Preserves is here demarcated and guarded in perpetuity.

The present extent of the reservation is marked with double lines on the game map (map 7). Nothing less than that area should be reserved, but I hold also the view that its boundaries need demarcation on a more scientific survey than has yet been attempted. For one thing it does not matter whether much of the reservation is tsetse-infested or not provided human habitation is not present to keep the tsetses infected; the survival of tsetse in this area alone will some day add much to its interest; but it is of some importance that its periphery, to be kept as a buffer, should where possible be free of tsetse or capable of being easily freed; so that when some day, in the future, development is arriving at its margins, we may avoid the outcry raised against the Zululand reserves that they are a centre and source of infection to the cattle-keeping areas outside. Again, as a first step in "management," it is important that we should study the requirements, general and local, of every species of east African game that can live in the area, and include in the area every amenity possible.

I have offered to carry out next year a careful tsetse survey of the Preserve (misleadingly called " Closed Reserve "), with its Sanctuaries and the country surrounding. The Botanist (Burtt) would take part in this survey and produce a botanical map, and the relation of the game to the vegetation and tsetse would be studied in conjunction with the Ranger. These steps, with the work we are initiating on game food and game habits in Shinyanga—on species all of which are found on the Serengeti as well—may constitute a useful contribution to the surveys required.

Meanwhile I hope that in the interests of the game, of science, of sport, of the Territory itself and of the world at large no corridors for cattle will be cleared to the Serengeti Plains. There are large areas nearer home which can be reclaimed to serve any increase of the cattle of Usukuma. As regards present mining developments, it is unlikely that with the price of gold ultimately lower many of these will be permanent. The game can in the meantime be preserved against the day when the Plains can be devoted to it wholly, and oxen, not game, be used for the feeding of labour.

The photographs of these plains which figure in the present paper were taken by Mrs. M. S. Moore, wife of the Game Ranger in charge, and herself an Honorary Ranger.

(h) Kiratu–Oldeani : or Inchi-Mpya, Northern Province.

(map 1 (upper part of central portion).)

A description of the fly belts and fly problems of the Mbulu district has been given already and the narrow fly band, which, following the Endabash stream, connects—or connected—the great *swynnertoni* fly belt of Eyasi and the Yaida depression in the west of the district with the belt bordering Lake Manyara to the east, has been mentioned (p. 380 above).

To the south of this Endabash fly band has lain the country belonging, hitherto, to the Erokh tribe, or Wambulu. Between its north and the highland forest area of the rim of the Ngorongoro Crater lies an area 300 square miles in extent, not mbuga but open and nearly open grass-country. It is itself subdivided by a narrow fly belt, in the main seasonal, which runs up along the Mrera stream from the north-west corner of Lake Manyara.

These grass-lands, and the country generally north of the Endabash fly

band, were unoccupied when the British took the country. The Wambulu "had been driven out of it by the Masai and, since the departure of the latter in 1903, they had been forbidden to return as the empty country was reserved for European settlement by the Germans." A boundary was fixed beyond which, to the north, the Wambulu might not settle. Beyond the boundary was the Oldeani area. At Oldeani there is to-day a limited European settlement. "The fly-free balance of this area, which amounts to approximately 300 sq. miles, appears to be eminently suitable for the use of the Mbulu tribes. Though the rainfall is comparatively low, it is sufficient for native crops: the soil is excellent and the grazing is everywhere good. . . . I recommend very strongly . . . that the area still unalienated be placed at the disposal of the Mbulu tribes" (Bagshawe, 1931).

The band of fly on the Endabash stream was a difficulty in the way of the above intention, but Mr. P. E. Tully, of the Veterinary Department, had already formed a plan for cutting a corridor through it, and himself, with the native authority, carried out the first contributory clearing—"Tully's Cut" —a most creditable piece of work. The whole scheme has since been developed by Gordon-Russell, formerly of the Tsetse Research Department, who has carried out further and adequate corridors through this belt, dealt with the band on the Mrera river as well, and opened up clearings to various infested waters, that are adequate, with the Endabash, Barai and Mrera, for the watering of the whole area. Generally, working with the Administrative Officers of the District, of whom he is now one himself, he has opened up for occupation by the Erokh the 300 square miles of country already described as fly free —with, owing to the narrowness of the fly bands, a minimum of work and expenditure. The work is nearly completed and the achievement has been a fine one.

(i) Kikoletwa, south of the Arusha-Moshi road, Northern Province.

(map 7, for Sanya.)

A scheme that might well be attacked, after survey, in 1937, is a break from a large mbuga to its south to the Kikoletwa river, south of the Sanya Plain between Arusha and Moshi, through a band of infested bush. It will enable the mbuga to be used.

(j) The great mbuga between North Kondoa and Masailand, Central, and Northern, Provinces.

(map 1 (upper part of central portion, along the junction of red and blue colouring).)

This, running southward from a point to the east of Ufiome Mountain and Galapo, past, and a few miles from Kikore, Kandaga and Itundwe, forms a broad barrier, fly free except for odd "islands," between the south Masai fly belt of *G. swynnertoni* on the east and the Kikore-Itundwe *morsitans* belt, lying below the Bereku scarp on the west. On a length of 30 miles or more it probably averages 5 miles in breadth—total 150 square miles—and the west-to-east clearings we are now, with the Administration, putting through north and south of Galapo and on the Kikore river will enter it and form cattle corridors leading to it. It can be entered also with still less work from points further south. The Kikore river corridor now being made by the Administration, the tribe and ourselves in co-operation eastward into the mbuga, and which it is intended to settle, is to be $1\frac{3}{4}$ miles wide by $4\frac{1}{2}$ miles long, and I have recom-

mended that next year, tribal funds being available, its head, at Kikore village, should be connected with the fly-free country of the Bereku ridge top with a corridor only 200 yards wide which would be used for the *night* passage of cattle. It is believed that this will be successful and that it will enable the settlers of the main clearing to bring in their cattle and utilise the mbuga as well. When (as we hope) the tsetses are expelled from the blocks of country between these corridors, a rich extent of valuable grazing will have been added to the assets of the tribe. The Harue water is being cleared to a distance of 1,000 yards round and will water large numbers of cattle, but further waters will doubtless need later to be supplied in the form of earth tanks, exactly as on the Huruhuru, and Findlay has indicated sites for possible dams. Meantime the first steps have been taken.

D.—THE SETTLEMENT OF THE AREAS RECLAIMED.

1.—TWO TYPES OF COUNTRY.

"Cultivation steppe" (German "Kultur Steppe") is ground that has been transformed by the presence of human settlement. Usually here it is heavily over-settled or, at least, over-grazed. It is cleared of trees and, annually, bared of grass. The transition from fair to bad—from mere settlement to soil erosion—may be seen in plate 18, fig. 2, to plate 20, fig. 1.

The second and contrasting type is the tsetse-fly bush, unentered by settlement or at most sparsely sprinkled with villages. It is well covered with trees, some of them of economic value, and it carries a fine stand of grass. Usually one can walk straight out of the one type into the other, and the strength of the contrast from bare earth to good grass cover may be visualised by consulting also the many bush photographs included in the illustrations of the present paper.

2.—THE POSITION AS REGARDS EROSION, AND THE NEED FOR THE EXPANSION OF SETTLEMENT IN THE LAKE PROVINCE.

In the fly-free, settled, "cultivation steppes" of Usukuma a very high proportion of the ground is cultivated and the whole is grazed at the rate of less than three acres to the ox, instead of, shall we say, at the rate of five, which possibly this originally good grazing might stand at the mouths of small beasts. In the same way numbers of sheep and goats wreak their usual havoc over the self-same ground.

To the country the result is disastrous. Every year the ground is bare of grass when the first torrential thunderstorms discharge, much is bare permanently, and although, owing partly to the gentler gradients, consequent gully-erosion has not become as spectacular as it has in Singida and Kondoa-Irangi, sheet erosion is everywhere rife and, probably owing to the heavy run-off, gully erosion is increasing, particularly on the granite.

Unobservant persons, or persons visiting the district once only, do not realise the seriousness of the position or the fact that ruination and abandonment, already in some spots taking place, can be the only ultimate outcome of a continuance of the present procedure. I myself, already interested in erosion, had occasion to walk and bicycle through considerable parts of the settled Shinyanga district in 1923–25. I recently spent a day in revisiting these areas by car. In the first period mentioned I noted that accelerated erosion was everywhere visible, but two places, one in Mwadui, where broken

rock had been bared, and one in Usiha, where incipient donga erosion was seen that was merely in advance of the rest, were specially noted as bad, and the second was photographed.

To-day neither of these instances would attract special attention, for each represents a type that has since become rife through the district. Comparison of the photographs referred to with the present position at the same spot showed a wholesale removal of soil.

Wash is the main agent. Wind-erosion, however, undoubtedly plays a large part. Sandstorms have of late years begun to take place and in October–December, 1934, every thunderstorm passing across the bared, desert-like ground of the chiefdoms of Central Shinyanga was preceded by a great red wall of dust and grit, several hundred feet high.

Not only is the soil removed. The manure deposited by the cattle on the land is now practically the sole source of humus. This, disintegrated by their trampling or the preceding rains, must largely go off on the wind or with the wash to the rivers.

Fig. 2 of pl. 18, pl. 19 and pl. 20, fig. 1, give some idea of the positions (*a*) in Shinyanga, (*b*) in parts of the Central Province.

As regards the cattle, it is true that very great numbers of animals die each year directly and indirectly from poverty and that a distant approach to a balance is thus struck between these and the available grazing. An actual balance is prevented by the fact that to save the herds from even more wholesale destruction the natives towards the end of the dry season drive them to feed in the fly bush, and so, though great numbers die through trypanosomiasis, the deaths are less wholesale than they would have been if the animals had had to face sheer starvation. The survivors, still over-many, are then replaced on the land and reinforced by the year's progeny. The balance is thus artificially maintained at a quite uneconomic level and the destruction of the country continues. Flat agriculture, without contour ridges, and ridges running downhill contribute to the effect.

3.—SOME OF THE OBJECTS OF ANTI-EROSION PROPHYLAXIS.

Some of the objects of anti-erosion prophylaxis must, therefore, be (*a*) to increase the annual slaughter or dispersal of the stock until it everywhere fits the economic carrying capacity of the country, (*b*) to replace the present sheer wastage of the surplus by a profitable use of the latter, (*c*) to increase the carrying capacity of the country to make the surplus less, (*d*) to get the fullest possible use out of the fine cattle-asset existing (i) for the improvement of the soil, (ii) for the improvement of the health of the natives, (iii) for their enrichment, with its sequel of accelerated civilisation and development, instead of, as is becoming the fashion, regarding these invaluable animals as a pest pure and simple.

4.—THE ACTUAL WORK SO FAR DONE.

Owing to a growing realisation of the seriousness of the position, the question has of late become a live one and efforts are being made by the various technical Departments concerned to contribute to the solution of the problem. An important result coming mainly under (*b*) above is in course of being achieved by the Administration and Veterinary Department, working together and aided by the monetary wealth which the Agricultural Department is bringing to the natives. This is the development of markets.

The Meat Rations Company, with machinery at Mwanza, is in effect as much an attempt to begin to solve a big east African problem as a commercial proposition, and, at the moment, it appears that with an increasing demand for dried meat the Company will be able to play an important part in the absorption of slaughter stock.* Further, a very large proportion of the huge sum received annually by the Bukoba natives for their coffee crops is spent in buying cattle which are killed for meat. A total of 22,812 head of cattle, valued at £37,980 was driven to Bukoba from Usukuma in the first nine months of 1934 (figures kindly supplied by Capt. J. D. S. Tremlett, Senior Veterinary Officer, Mwanza). Yet further, butchers' shops are now opening up everywhere amongst the Wasukuma themselves who, with the money from their cotton crop, are willing to buy meat though they will not kill their own cattle. How small the beginning is relatively to the need was shown by the desperate appearance of the whole country-side again this year and the great numbers of cattle that were driven to feed in the tsetse bush, the rains having ceased early, but at any rate it is, at last, a beginning, and an encouraging beginning. In 1930, markets were only in process of establishment. In 1934 (only to September, inclusive), 104,055 head were sold, following a steady annual development due to better organisation and improved native purchasing power (Tremlett).

The experiments in the cure of erosion and improvement of pasture now in progress at the Veterinary headquarters, Mpapwa, should be mentioned. Their results are most striking.

As regards the work of the Forest Department and Administration, Mr. C. McMahon, when in administrative charge of Shinyanga, pioneered a start with the formation of wind-breaks, and planting has taken place since in the neighbouring districts of the Province, *Cassia siamea* being the chief tree used. Against the steady winds of the late dry season wind-breaks closely spaced may be useful. Against the swooping thunder-winds that, swirling the soil steeply hundreds of feet into the air, have been carrying it off westward into the tsetse bush, they are likely to be much less useful. The remedy is to prevent the exposure of the soil.

A further and very important development concerns the fitting of the ground to carry its fullest quota of cattle without deterioration and the utilisation of the animals in their proper place in a sound agricultural scheme. Starting with two model plots at Ukiruguru, south of Mwanza, the Department of Agriculture has embarked on the development of the idea of individual native holdings for the employment of permanent methods. Rotation of crops is employed, feed is grown for the cattle, the latter are kraaled at night in a byre, the manure resulting contributes to a compost prepared on proper lines and is used for the crops. Organisation on these lines has been applied in country reclaimed from the tsetse in Buhungukira and is being started on a large scale by the Department of Agriculture in Uzinza (West Mwanza), (map 1) and at Lubaga (in Shinyanga), (map 2).

Contour ridging is everywhere being encouraged.

The part played by the Tsetse Research Department in the present connection has been (*a*) to learn to reclaim land from the tsetse; (*b*) actually to reclaim land in Shinyanga and to assist the Administration to reclaim it also elsewhere—for the extension of grazing and the more economic dispersal of the cattle, with a view to relief of over-grazing elsewhere; (*c*) to urge, and

* Since this was written, this enterprise has (I understand) been closed down.

prepare for, the regulated settlement of the land it reclaims with a view to averting over-grazing and erosion within it.

The tsetse fly is performing an invaluable function (as Mr. A. J. Wakefield, now Deputy Director of Agriculture, was one of the first to stress) in holding great areas of excellent land in reserve, and the justification for reclaiming it is that such efforts are being made to rectify permanently the balance of the cattle and their grazing, and to introduce better agricultural methods as will ensure that the country will not be maltreated and ruined when we have taken it over from the safe custody of the flies.

5.—PAST SETTLEMENT OF THE AREAS RECLAIMED.

The position, when the work was first begun in Shinyanga, was that a rout was in progress and that it was in any case a pure experiment whether we could, without force, which we were determined to avoid, induce settlement to come into the places reclaimed.

A few headmen were found who were willing to return to their old homes in the hope that their people might come to them. Otherwise inducements were necessary to start the ball rolling. Tax was for a time remitted, approximately 200 acres were ploughed in all at Lubaga and as a three-mile strip along the road thence northwards to the Ninghwa, huts were put up in suitable positions at intervals and settlers were invited in. Luka, one of the headmen, was particularly active in seeking adherents and the area gradually became occupied. The growth of settlement subsequently has been that of a snowball in the areas reclaimed then and since, and it is many years now since we were able to discontinue inducements—apart from providing thatching grass and assistance in transporting their grain-reserves in the case of approved settlers. In fact, nowadays we have only to commence work on a piece of ground for long-ousted headmen to come and repeg their claims and for commoners to start building huts. It is a testimony to the faith in us which, based on experience, has grown up in the minds of the natives, but, where our activities are only experimental, we find it embarrasses the work.

6.—THE WRONG AND THE RIGHT WAYS TO SETTLE COUNTRY RECLAIMED.

(a) The wrong way.

The way that was necessary at first has now become definitely the wrong way. Since the rush started there has been no means of keeping the intending settler away from land which his effort had contributed to free from the flies, and the tribal customs encourage the piling of settler on settler : a native has only to leave a piece of a field previously cultivated by him uncultivated and somebody else may seize on it. The result has been that in the last three years the more popular portions of the areas we have reclaimed have become as much threatened with erosion as the general cultivation steppe.

The wrong way to settle new ground is to place no limit (*a*) on the numbers of the settlers coming in, (*b*) of the cattle using the area.

(b) The right way.

Opinions may differ on the details of the method to be adopted, but they cannot differ on the necessity of regulating entry to fit the capacity of the area. The excellence of the individual-holding experiment initiated by the Department of Agriculture has been emphasised above, but the training, equipment

and launching of each family costs a good deal of money (lately estimated at £36), and it is doubtful whether a scheme for the filling of the great new areas so badly needed with holdings of given size can (i) be sufficiently financed, (ii) be pushed on fast enough to meet the urgent situation existing—for the destruction of the cultivation steppe from which the settlers would be drawn is proceeding at a quite rapid pace. There are difficulties also that come from the conservatism of the natives themselves. Thus those adopting new innovations are regarded with considerable odium. To quote from a letter of mine on the subject:—

"The position. There is an enormous area here and in Usukuma generally which is being destroyed by bad agricultural methods, over-grazing (especially) and consequent erosion. It is being *rapidly* destroyed. . . . There are huge tsetse areas alongside, offering, in conjunction with the areas under occupation, all the room these people and cattle could require for farming on rational lines. . . .

"One of the big practical needs, then, is for a system that will quickly settle all areas reclaimed but do so without overcrowding and without prohibitive expense—and which will thereby more and more relieve the congestion in the areas settled already. With it would go, in both old and new settlement, such simple but important anti-erosion measures as the Department of Agriculture has already so usefully inaugurated. 'High farming' should be aimed at also and the sooner its foundations are laid the better, but it needs much less than high farming to save the immediate situation and, as such farming will demand a complete revolution in native ideas and customs and will therefore progress relatively slowly—over obstacle after obstacle discovered, studied and overcome—it must gradually but steadily follow from tentative beginnings made now.

"The intermediate measures suggested are these. Admission of settlement into areas reclaimed, on present native lines but on a quota basis. The scheme was suggested a year ago by one of my Field Officers [Wheeler], and Mr. R. de Z. Hall has dealt with the question independently. . . . In this scheme the number of people that each village area in the district can carry without harming the land is assessed and recorded and the village boundaries are finally fixed. This is followed by the gradual scaling down of the population of the over-populated 'gungulis' as opportunity offers and the encouragement of immigration into those which have not yet reached their quota allowance. When the maximum is reached immigration is made to cease. Where there is fly bush reclaimed there will follow a gradual withdrawal of the surplus population of the old settled areas to those newly opened up. But these new areas will not be devastated, as settlement will be strictly controlled according to the carrying capacity of the land, the surplus of the young generation will be moved on, and the number of cattle will be limited to fit the grazing capacity.

"The above, enforced, will have an early and far-reaching effect towards the cure of erosion and the mending of the whole present unsatisfactory situation in Usukuma—and that without breaking strongly with native ideas. . . .

"On the ground-work and under the shield provided by this 'rescue' measure, I would raise the structure of the individual holding, feeling our way, to make no mistake, political, propagandist, or other.

"Any very wide departure from the lines just sketched out is likely to be far too expensive to apply as a general measure and also to fail as leaven.

"We are convinced that the Government must carry the people with it,

and that only by the provision of an easy transition like that indicated above will it be able to do so. . . . The ordinary natives would be faced with a small step only at a time, and those even who had made the greatest advances would not appear too unique, for a transition would exist between them and the least advanced and public opinion would not be aroused against them—and, through them, against the scheme."

It is necessary " to save the settled country from its present growing destruction and advance the natives without (i) alienating their sympathy for the schemes that will be adopted, (ii) building up a new class apart that will not fit into our policy of tribal organisation and indirect rule."

7.—AN ATTEMPT TO PREVENT OVERCROWDING, PENDING A DECISION AS TO POLICY.

When the Outer Circle was thrown open to settlement the Department was determined that the pick of the land—the Ninghwa stream valley—should not be crowded as had been some of the country reclaimed earlier. Accordingly in 1934 nearly fifty individual holdings were laid out in the valley, each farm so sited that it had a gradation of soil from the red loam of the higher country to the fertile silt of the valley bottom, a stream frontage and an outlet to a farm-road leading to motor-roads behind. Nor was it forgotten that in time to come large herds of cattle belonging to other settlers would need the Ninghwa waters, and so spaces were left for cattle-roads and cattle watering-places.

The boundaries of the holdings were marked with manyara cuttings.

After consideration, it was decided that, due allowance being made for the advance in agricultural methods (*i.e.* the use of the plough) that might be expected in the near future and for provision for a " wood-lot," etc., 25 acres for each holding with the right to 25 acres of grazing commonage, would be a suitable size and a size that later, if necessary, might be desirable.

After a few preliminary difficulties had been overcome, the idea caught on, and the holdings were quickly taken up.

Not much attention was paid at the outset to teaching the settlers good agricultural methods, although seed was distributed and a demonstration holding established with the co-operation of the District Agricultural Officer. It was hoped that the Department of Agriculture would do this and that when the last wandering fly had been driven from the area and cattle could safely be kept, then, if not before, that Department would step in and take over completely.

It was the primary concern of the Tsetse Research Department to ensure that, in the period before an official decision was taken on the much-needed regulations, the land should not be ruined.

E.—WATER SUPPLY.

It has not been enough to drive the tsetse out of an area attacked by us. We have at the same time, in each instance, had to provide permanent water, where this was absent, to make the block inhabitable by settlers. The provision of water has been especially necessary to enable cattle to use the great open mbugas which we have opened up and in which, unless at the widest intervals, no permanent water has been present. Three methods in all have been used.

These three methods have been (1) the coffer-dam, (2) the earth-tank,

(3) in a single instance, which might be extended, the utilisation of the catchment from the surfaces of large rocks. These methods are illustrated in pl. 16; and the making of all three is described on pp. 422 and 423 below.

F.—SOME RECLAMATION TECHNIQUES.

1.—THE TECHNIQUE OF CLEARING FLY BUSH.

(a) Experiments in methods of clearing.

Experiments in methods of clearing were carried out first in Kilosa and Shinyanga in the years 1921–23 when piling and slicing were evolved. Poison for killing trees had been experimented with earlier (Swynnerton, 1921). It was obvious that much work was needed to bring our methods of clearing to perfection, and Napier-Bax took charge of the task as soon as he came to the Department. He worked in Itundwe from 1928 to 1929 on methods of clearing and continued his experiments on an extended scale after his transference to Shinyanga. At the latter place twenty-six 20-acre and two 5-acre plots were laid out. They were dedicated to the trial of various methods of clearing and the ascertainment of costs. They included experiments in :—

(i) Poisoning.
(ii) Termite attack.
(iii) Ring-barking and frilling.
(iv) Felling.
(v) Felling and piling.
(vi) Dealing with ilula (gall-acacia) bush.
(vii) Dealing with thicket.

Further plots have since been added for special purposes.

We published as a Departmental pamphlet in 1932 so excellent an account from Napier-Bax's pen of the methods evolved, that, seeing that many of those who read the present report will not have seen it, it will be useful to quote from it freely.

(b) The rôle of bush clearing in tsetse control.

" While bush clearing will always, in considerable degree, be necessary in campaigns against tsetse, it will in the future go hand in hand with other methods to a greater degree than it has in the past. Total clearing will be used chiefly for breaking the country into blocks within which the flies will be dealt with by other methods, of which partial, discriminative clearing may be one." (Swynnerton, preface to Napier-Bax 1932.) The following passages in inverted commas are quoted from Napier-Bax's paper.

(c) The various types of clearings.

" Clearings may be broadly classified into Permanent Barrier Clearings, Reclamation Barrier Clearings and Settlement Clearings. The first may be combined with the last [only] provided abundant extra width is available.

(i) *Permanent barrier clearings.*

" These are essentially defensive methods and are designed to hold up a fly advance. . . . Therefore such barriers would have to remain effective for a considerable period and should be made as permanent as possible by employing the most thorough methods of clearing." The so-called " permanent " clearing

is that in which every means available is taken to kill or suppress the growth from the stumps of the felled trees and thickets. Here " piling " and " slicing " are resorted to and the cost is consequently comparatively high.

(ii) *Reclamation barrier clearings.*

" These are very similar to permanent barrier clearings, except that they are designed as an aggressive weapon against country in possession of the fly. They are made with the object of dividing the country up into blocks, each of which forms a separate entity and between which the passage of flies is checked. Steps can thus be taken to drive fly from a single block without fear of re-infestation from neighbouring fly areas.

" As the reclamation of the blocks proceeds and a sufficiently big area is consolidated behind the line of attack, regeneration may be allowed to take place in the first clearings. . . . No settlement should be allowed in reclamation barrier clearings." A reclamation clearing is shown in pl. 18, fig 1.

(iii) *Settlement clearings.*

" The least permanent, and therefore the cheapest form of clearing, can be employed in these, the influx of population and livestock impeding regeneration. . . ."

The " temporary " method of clearing, to be used in connection with settlement, or sometimes in a reclamation barrier clearing, is one in which felling only—of trees and thickets alike—is employed. Between this extreme and the " permanent " clearing there is the " semi-permanent " type which is most useful in certain circumstances—often in a reclamation barrier clearing. In this case expensive " piling " is omitted but " slicing " and " low ring-barking " (cheap measures) are used.

(d) Methods of killing trees.

(figs. 27–29.)

(i) *Ring-barking.*

(fig. 27, 1 & 2.)

" This method of killing mature trees is widely known, and is practised by the native in his cultivation. It consists in removing a strip of bark from the circumference of the tree trunk, causing in many species (*e.g.* Acacias) death by slow starvation. . . .

" In its fight for life, a tree will endeavour to callus over the ring-bark, the upper and lower edges of the cut gradually growing together. If the ring-bark is of sufficient width (nine to twelve inches), the tree will die before it accomplishes this. . . .

" The phloem and cambial layer are vital factors in the internal economy of the tree and these, therefore, must be cleaned carefully from the ring-bark. Although the outer bark may be broken away from the surface of a tree, yet, if what is known to natives as 'kamba' is allowed to remain, the tree will continue to live and will gradually repair the damage. Often the bark is irregular and fissured, so that it is impossible to insert the blade of the axe into the crevice. . . . Such a tree is left incompletely ring-barked and consequently recovers. This is an extremely common fault when natives are left improperly supervised. . . .

" To ring-bark at approximately waist-height is most convenient, but the lower it is done, the more efficacious it becomes. . . .

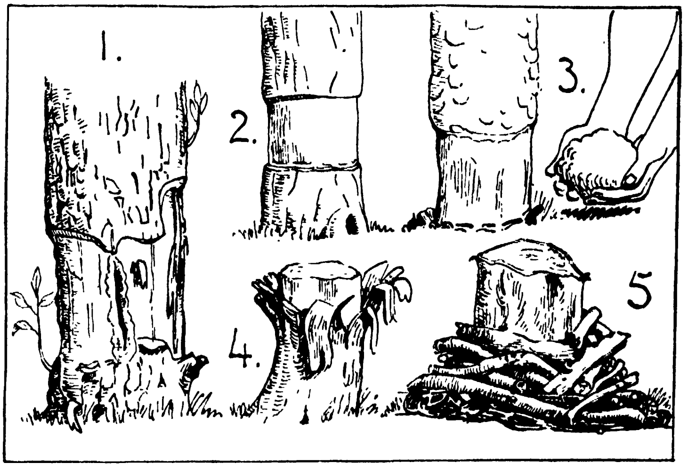


FIG. 27.—Bush-clearing technique.

1. A badly ring-barked tree. The site has been badly chosen, including, as it does, a slit in the tree from the sides of which it is difficult to remove the bark; the barked strip is unnecessarily wide; and, at that, the work has been badly done, leaving strips of cambium, which, with a piece of bark not removed at all on the left, will form connections across the barked strip and keep the tree alive. 2. An *Acacia spirocarpa* tree ring-barked correctly. 3. A *Commiphora* tree prepared for the admission of termites. It is roughly ring-barked near the ground, some light cuts have been made in it close to ground-level and a handful of earth is about to be thrown up against its base. The termites do the rest (see fig. 28). 4. Slicing. An *Acacia spirocarpa* tree felled and then "sliced." Such a tree dies in the rains. (This is applicable only to mature acacias.) 5. A stump piled correctly for killing by burning. Short lengths of wood have been used and the pile is tight and compact.

" A great disadvantage in the method of ring-barking is that some years are likely to elapse before the tree falls. Even death of the upper part of the tree will not necessarily follow within twelve months, and it may be three or four years [or more] before the whole tree falls."

(ii) *Slicing.*

(fig. 27, 4.)

" The bark is sliced down from the top of the stump for about nine inches, leaving the strips attached to the trunk at their base. A trough is thus formed around the naked wood, which tends to catch the rain and promote fungal growth. The use of slicing is limited to fully grown trees."

(iii) *Piling.*

(fig. 27, 5.)

" Piling and burning may be employed with success on many of the species which sucker and coppice, and are not, therefore, susceptible to ring-barking.

" The tree is first felled, and the bark of the stump slashed at ground-level. It is not necessary to make a clean ring-bark, a few strokes of the axe suffice. Grass is then piled round the base, small sticks follow, and on these are piled

larger pieces of wood. . . . *The pile must hug the stump closely and the wood be cut in short lengths of twelve to fifteen inches.* Branches thrown on undivided are useless. The wood should lie flat and not be piled on end, as in the latter case the pile is liable to fall apart on firing. . . .

" It is quite unnecessary to make the piles large; they should be conical in shape and from one to two feet in height, depending on the size of the tree.

" In the winter (late dry season) when the grass is dry and ready to burn, and there is a good wind, the veld should be fired, when the piles will catch alight and the stumps of the trees and their roots be severely charred."

(iv) *The utilisation of termites.*
(fig. 27, 3.)

" The bark of Commiphoras is very distasteful to termites, but the wood, on the contrary, is much liked by them. The tree is therefore ring-barked at

Fig. 28.—A *Commiphora Fischeri* tree bared to termites, as shown in fig. 27, 3, and killed by them.

ground-level, care being taken that the bark is removed right down to the level of the ground. A succession of single cuts with the axe, encircling the tree, is then made at the point at which the trunk enters the ground and two

handfuls of earth thrown over the cuts to give cover to the termites. The cuts will encourage the termites to start work, as they apparently prefer entering at the end wood.

"It will only be a matter of a few months before the tree falls and the termites proceed to eat out the roots [fig. 28]. Their habit of continuing the attack upon the roots is important, as many of the Commiphoras coppice, and sucker freely if merely felled."

The method was discovered in 1926–27 when clearings made in *Commiphora* wooding in the Kondoa and Singida districts, and piled, were not burned immediately. When we came to burn them we found that the termites, working in and under cover of the piles, had destroyed all but a small percentage of the trees.

(v) *Poisoning.*

(fig. 29.)

(α) *The poison.*

FIG. 29.—A tree correctly "frilled" for poisoning; the bottle, with a drawn-glass tube through the cork, used as container for the poison; and an axe of the type found best for use in the hands of natives for clearing bush.

" Extensive experiments by the Tsetse Department with a large number of poisons have shown that arsenic pentoxide is the most successful. This is sold in hundredweight drums in east Africa by many agricultural firms and should conform approximately to the analysis : 83–85 per cent. Arsenic Pentoxide.

" It is essential that the term ' granulated ' should be used in the specification to avoid the possibility of being supplied with the fused type of article, which is extremely likely to be insoluble in water.

" The strength of the poison to be used depends on the species of tree, and reference will be made to this later.

" In mixing for use, boiling or very hot water should be employed. The operation may be carried out in a paraffin tin. Care should be taken not to inhale the fumes, which are poisonous, and for this reason it is best to mix the liquid in the open air. A sediment of greyish colour will be found in suspension, due to commercial impurities ; but as arsenic pentoxide is itself highly soluble in water, it is quite unnecessary to keep the tin stirred when applying the poison.

" There is a strong corrosive action on most metals, so that it is advisable to wash carefully all metal utensils used after each day's work."

A more detailed account of Napier-Bax's poisoning experiments is given in appendix 8. This may be valuable to future experimenters as listing the methods and poisons that were discarded.

(β) *The season to apply the poison.*

" Experiments have shown that the summer, when the trees are in leaf, is the best time to apply the poison in this country. At that period there is a much greater movement of sap in the tree, and the poison is consequently transported more freely."

(γ) *The method of application.*

" Root augering.
Base augering, referred to simply as ' augering ' in these notes.
Swabbing.
Frilling.

" The ' frill ' method has been found to be the easiest, cheapest and most successful method of application.

" A series of cuts are made with an axe around the base of the tree, as level as possible and as near the ground-level as practicable, say four to six inches above it. Each cut overlaps its neighbour, so that a continuous incision is made around the whole circumference of the tree. The cuts should be deep enough to penetrate well into the wood through the bark, but not more than a single stroke of the axe should be necessary to make each cut. It is important to frill near the ground, as it has been found that the movement upwards of the poison is much greater than the downward movement. Again, the lateral movement is poor, so that care should be taken that no unpoisoned strips are left, but that the circle of poison is continuous. If a fissure in the trunk interrupts the circle, a single cut or more, as necessary, should be made above or below the general line of incision, at the end of the fissure, so that the tree is completely girdled in spite of the break.

" The best instrument for introducing the poison into the ' frill ' is a beer bottle, fitted with a cork and a glass tube through the latter that is drawn to a point at the end. The poison is dribbled in all round through this. If handled with care, breakages are infrequent and also there is no trouble from corrosion.

Neither root augering nor base augering is a success.

There is no intrinsic difficulty in base augering savanna trees, but this method fails when the poison is introduced. A barber-pole effect is almost invariably produced. The *vasa* ensure a good vertical distribution of the poison but the lateral spread is very poor, with the result that only the strips situated above and below the holes are killed, other strips in the spaces between the holes remaining healthy.

Swabbing is a laborious and wasteful method. The tree has first to be felled and the stump then swabbed. The combination of felling and poisoning is nevertheless highly useful where an immediate yet permanent cleared effect is desired.

(δ) *The strength of the poison.*

" As has been mentioned, the strength of the poison will depend on the species of tree. In general it will lie between three to ten pounds per gallon of water.

" A careless boy will use twice as much poison as a more careful one, and unless headmen in charge of the operations exercise strict supervision, the cost will be much increased.

" Results. Within the course of a few days the leaves will be seen to brown and die, death of the branchlets will follow rapidly, which will in due course be followed by death of the whole aerial portion. Death of the roots follows more slowly."

(ε) *Low strength poisoning.*

Several field experiments have been carried out by Napier-Bax in " low-strength poisoning," the object being to defoliate or kill the aerial portion of the tree with a very low strength of arsenic pentoxide, but to avoid killing the roots. Country essential to the fly might thus be made temporarily unfavourable without doing lasting damage to the bush.

A strength of poison of 1 lb. to 2 lb. per gal. is quite sufficient for the purpose (it may be found after experiment that lower strengths still can be used) and the cost works out at about 9*d*. to 1*s*. an acre, in ordinary Shinyanga-type thorn-bush (pl. 5, fig. 1, and pl. 14, fig. 1), not including white supervision.

Regeneration after the treatment is slow and from the entomological aspect these experiments have been promising. For the immediate result on the wooding, compare pl. 14, fig. 2, and for that on the flies *see* p. 272. The defoliated area becomes a feeding-ground and with its extension the flies disappear.

(ζ) *Antidotes for arsenical poisoning.*

" Arsenic pentoxide is a deadly poison and should be handled with the greatest care; all drums and utensils should be kept under lock and key.

" It is advisable to keep a supply of fresh water in the field and insist that all labourers wash their hands on completion of the day's work.

" Should a drop of poison be splashed into the eye, the man must lie flat on his back and the eye held open and irrigated for half a minute or so with fresh water, when only temporary discomfort will result. Tenderness of the hands may be caused through the poison penetrating under the finger-nails, and for this reason labourers must be instructed to take care not to spill the liquid over themselves and to wash with particular care under the nails. . . .

" In all cases [of internal poisoning] vomiting must first be caused, and a strong solution of salt and water will generally suffice. The antidote is prepared by mixing a teaspoonful of perchloride of iron in a tumblerful of water and adding about half a teaspoonful of bicarbonate of soda, well stirred and taken immediately. This antidote, ferric hydroxide, should be kept in the form of

perchloride of iron, put up in well-stoppered bottles; by this means it is possible to obtain a freshly precipitated solution of the antidote in the field whenever it may be required."

(e) Destruction of scrub and thicket.

"It is possible to destroy thicket by digging it up by the roots, or again, poisoning the exposed roots with a high concentration, but neither of these methods can be practically applied owing to their great expense. Spraying with poison has also failed. Death of the leaves and the more delicate stalks ensues, but the bush soon reshoots with great vigour.

"No cheap and yet satisfactory method has been found that will kill scrub. Where bushes are large, however, they may be cut down and piled like trees. It is of no use merely slashing them and leaving the debris lying indiscriminately over the ground in the hope that when fire comes it will damage the root system. . . .

"Smaller scrub is merely slashed, and fierce grass fires will do much towards keeping new growth suppressed" (Napier-Bax, 1932).

I found ordinary coarse salt being used in the United States of America for the destruction of the wild currant bushes that were a host for the White Pine blister rust. For our thickets it would be much too expensive, and the natives, discovering it, would leave little.

(f) Methods of killing and effectively suppressing species belonging to some common genera of savanna trees.

In table 59 (p. 414), prepared by Napier-Bax, are given methods of killing and effectively suppressing species belonging to some common genera of savanna trees.

(g) The difficulty of killing species of *Combretum*.

Combretum is one of our commonest genera and includes a great number of species. All these species agree in the fact that they are exceptionally difficult to kill. They always shoot afresh below a ring-bark; when they are piled high and thoroughly burned suckers commonly appear from points in the roots which the heat of the fire has not reached; if they are stumped the same thing is liable to happen. And *Combretum* is far more resistant to poison than most other tree-genera. With it to a lesser extent may be classed *Albizzia Harveyi* and *A. sericocephala*, *Protea* spp., and *Terminalia*.

Research by Prof. Priestly of Leeds University had indicated, however, that the vessels of the trees instead of containing liquid under tension as is the common view, contain water vapour. He had found that when a tree is cut with an axe, air is at once absorbed by the severed cells—a "breath," so to speak, is taken and in the African tree *Haronga* one can actually hear what is possibly this process. The air thus taken in acts as a buffer against poison applied afterwards. If, on the other hand, the cut is made under water, the water is inspired instead. And so with poison in solution. This was interestingly borne out by Napier-Bax at Itundwe when, the cuts being made under water mixed with eosin contained in a beeswax bath built round the stem, the bright red colouring matter in a very few minutes after reached and stained all the foliage to the very top of the tree.

The method has not yet been followed up owing to the pressure of other work and some difficulty in providing an adequate poison "gun." The forms under consideration are a chisel type with a spring and one that is worked pneumatically.

(h) Making clearings.

(i) *The season.*

" The best clearings can be made only if a definite plan of reclamation, extending over several years, is worked out beforehand. In this way, due regard can be paid to such points as the presence of dry wood in the piles, etc.

" The periods in which an operation, requiring such a large amount of labour, can be carried out, are limited to those during which the native is not working on his shamba, *i.e.* mid and late winter (dry season).

" However, the earlier in the dry season a start is made, the better, as the

TABLE 59.

Methods of killing and effectively suppressing species belonging to some common genera of savanna trees.

N—Denotes negative results, *i.e.* the method is unsuccessful.
K—Denotes that the tree is killed.
S—Denotes that although the tree is not killed, yet it is so hard hit that it is incapable of shooting properly for some years.

Scientific name	Ring-barking	Felling and slicing	Piling	Termite attack	Poisoning	Remarks
**Acacia* spp. Mature	K	K	Unnecessary	Not known	K (7 lb.–1 gall.) Roots die slowly	Slice for rapid results. Ring-bark for cheapness.
**Acacia* spp. Immature	N	N	K	Not known	K (7 lb.–1 gall.) Roots die slowly	
Isoberlinia and *Brachystegia* spp. Mature	K	Not known	Unnecessary	Not known	K (10 lb.–1 gall.) Roots die very slowly	
Isoberlinia and *Brachystegia* spp. Immature	N	N	Not known	Not known	K (10 lb.–1 gall.) Roots die very slowly	
Commiphora Fischeri	N	Not known	Unnecessary	K	Unnecessary	
Commiphora pilosa	N	Not known	Unnecessary	K	Unnecessary	
Commiphora Schimperi	N	N	K or S	N	K (10 lb.–1 gall.)	Observation tends to show that termite attack is only partially successful. But a considerable percentage is killed.
Commiphora Stuhlmannii	Not known	Not known	K or S	Not known	K (10 lb.–1 gall.)	
Commiphora ugogensis	Not known	Not known	K or S	Believed susceptible	K (10 lb.–1 gall.)	
Dalbergia melanoxylon	Not known	Not known	K †	N	Unnecessary	
Albizzia hypoleuca	N	N	N	N	K or S (10 lb.–1 gall.)	
Lannea humilis	N	N	K or S	N	K (10 lb.–1 gall.)	See remarks on *C. Schimperi.*
Combretum spp.	N	N	N	N	N	The *Combretum* can often be fairly well suppressed by poisoning, but the effect is not certain. (10 lb.–1 gall.)
Schrebera Kiloneura	N	N	N	N	N	ditto.
Ostryoderris Stuhlmannii	N	N	K or S	N	Not known	

* The *Acacia* trees that have been poisoned successfully are *A. spirocarpa*, *A. Benthamii*, *A. senegal*, *A. Kirkii*, *A. formicarum* and *A. Seyal*. The results of ring-barking have not been noted yet on species other than *A. spirocarpa*, but general past observations suggest that these methods can be applied successfully to the mature trees of the other species of *Acacia*.

† This tree should be piled, but it is unnecessary first to fell it. If the rough ring-barking at the base is carried to a sufficient depth to expose the black heartwood, this will burn fiercely and the tree will accordingly fall.

wood in the piles will have much longer to dry out properly, and the fire will be proportionately more effective. Further, with the advance of the season, the water problem becomes ever more acute, and it may be a matter of extreme difficulty to maintain an adequate supply for a thousand or more labourers late in the year.

" There is often a strong temptation to burn off the grass before clearing, in order to facilitate the work, but this should be resisted, as it will lead to piles being made with insufficient grass. . . . On the other hand, felling only, on the burnt ground, might be carried out the first season and piling and burning of the piles delayed until the second. There would be an abundance of dead wood available for the piles, and, provided piling was done early, before the grass had grown long, it would be ideal."

(ii) *Laying out the clearing.*

" In surveying the line to be defended, physical factors which may be worked into the scheme should be utilised, *i.e.* mbugas entailing no clearing or very light clearing; scarps; dense, wide thickets through which the fly will only find its way with the aid of man and animals and the weak points of which may be defended. The complicated peculiarities of the various species of fly and their habits will influence the final decision as to the best line of clearing and will necessitate the expert advice of an entomologist. Too often, in the past, strict attention has not been paid to the laying out of the clearings. An approximate, rather than an exact, line has been followed. Besides the obvious loss of time and labour entailed in such haphazard methods, there is the serious danger of making the clearings too narrow in parts by a gradual convergence of should-be parallel lines.

" Second-hand army compasses are sold by reliable firms at a reasonable figure and, if the lines bounding a clearing are started by a white officer, an intelligent native will have no difficulty in continuing them."

(iii) *Width of permanent and reclamation barrier clearings.*

" This is a matter which must receive very careful consideration, and will depend on a number of factors, such as the species of fly, the topography of the country, etc. An expert who has a wide experience of various fly belts and conditions can, alone, properly judge what width is sufficient."

(iv) *Standing trees in clearings.*

" No effort should be spared in making clean clearings. It is not at present possible to deal economically with certain species of trees such as Baobabs, but, just because a tree is large or of hard wood, it should not be left. The larger and more conspicuous the tree, the more danger there is that fly will use it as a stepping-stone from one side of the clearing to the other."

(v) *Wave attack.*

" The procedure of ring-barking Acacias, two or three years before the remainder of the trees in a clearing are dealt with, is an elementary form of wave attack, the idea being to deal with the trees in the order of the length of time that it takes them to die, thus synchronising the death of all in (more or less) a single year. Another aspect of wave attack is the use of an unskilled main gang preceded by specialist gangs following each other at short intervals through the clearing, each confining itself to its own special methods and appropriate species of tree. . . . Specialist gangs should be restricted to poisoners,

or those applying the more complicated method of attack, which it is not feasible to teach the main gang. . . ."

(vi) *The supervision of clearings.*

"*Adequate supervision of clearings is most essential.* There should be a sufficient number of white officers as well as native headmen. No white officer, even aided by a small expert staff, can be expected to supervise properly more than five hundred natives, as not only has he to see that the labour is working reasonably well, but that it is carrying out efficiently the particular method of clearing that is being employed. This latter point is particularly important during the first few days, when the men are new to the work.

"It is most desirable that there should be a few permanent native assistants (one per hundred natives is the minimum suggested) who are well acquainted with all methods of clearing, including the more difficult, such as poisoning. These would instruct the headmen in the first place and later act as general supervisors. . . .

"As the work proceeds the tribal leaders present should also be trained in the work and assume their responsibilities.

"It is advisable to bunch the gang to a considerable extent, as in this way a greater part of it will come under the immediate control of the headmen, and also the labour has been found to work more happily when close together. One man per yard of front is a suitable espacement."

(vii) *Tools.*

"Experiments at Shinyanga prove that raw labour will clear sixty per cent. more country in a given time, armed with European tools, than with its own primitive weapons, in spite of the fact that scarcely any native can swing a European axe correctly and that he is extremely slow in picking up the knack.

"The type of axe fitted with a ring for the handle to pass through is greatly superior to the ordinary flat pattern, to which the handle is difficult to fit and keep in place. A light axe ($2\frac{1}{2}$ to $3\frac{1}{2}$ pounds) has been found the most suitable [fig. 29].

"A panga [bush cutlass] should also be supplied for slashing the brushwood.

"It is important that all tools should be kept properly sharpened, and a good plan is to halt the gang on its way to work each morning at a stony spot, so that each man may sharpen his own axe and panga. Alternatively, grindstones should be available, or a special section be detailed to sharpen tools on flat stones."

(viii) *The rôle of fire.*

"Fire plays an important part in the making of clearings, but its use is not merely confined to the making of new clearings, it extends to the maintenance of old ones. Regeneration is always taking place, the effort of Nature to repair the damage done by Man.

"The question of regeneration is not of so great importance in reclamation barrier clearings where attack is being pressed vigorously, their active lives being, in any case, short, but in permanent barrier clearings it is of primary importance. These can be only kept effective by sweeping them annually with a fierce fire. The alternative, regeneration, results in an increasingly ineffective clearing, or entails expensive reclearing. . . .

"For firing operations, a sunny day, with wind of gale force, must be chosen if possible, and the fire put in between ten and eleven in the morning when the dew has dried off."

(i) The cost of clearings.

" The cost of making clearings depends on the efficiency of the labour, the wages current in the district, the type of country through which it will pass.

" In the past, most clearings have been made by tribal labour, and this, while naturally the cheapest, is at the same time the most inefficient.

" With paid labour better results can be obtained, but the final cost depends on the wages paid, which fluctuate between thirty and fifty cents per diem.

" With regard to the type of clearing that is to be made, table 60 illustrates how the cost increases with the more permanent type.

" The density of bush that has to be cleared will, of course, influence to a very great extent the final figure. The following figures are based on a common savanna type of country, *Acacia–Commiphora*, supporting one to two hundred trees per acre, besides a number of large bushes (*e.g.* pls. 5, fig. 1; 13, fig. 1; 14, fig. 1; and (acacias) fig. 3).

TABLE 60.

The comparative cost of different types of clearings in *Acacia–Commiphora* country.

Method	*Cost per 100 trees in Shs.	Remarks
Felling . . .	0·65	Trees and large bushes.
Ring-barking . .	1·17	100% mature Acacias only with consequent high relative cost.
Felling and piling .	1·29	Trees and large bushes.
Poisoning † . . .	2·50	Strength 10 lb. per gallon. Landed cost of poison 50 cents per lb.

" * Figures worked out on the basis of labour at 40 cents and headman supervision at Sh. 1/- per day of eight hours. All work done with European axes.

" † Included in this experiment are all the common savanna species at Shinyanga except the Acacias, which were dealt with by other means. The greater the girth of the tree the more poison used, with corresponding increase in cost.

TABLE 61.

The labour necessary to make one mile of clearing, 1,200 yards wide, in savanna wooding of *Acacia–Commiphora* type (dry thorn-bush).

Labour	Method	Men/days
Tribal	Felling and piling	7,000
Paid	Felling and piling	3,000 to 5,000
Paid	Felling	1,000 to 2,000

Note.—All work with European axes.

" General note.

" When studying the above costs, which do not include white supervision, the reader must bear in mind the essential difference between anti-tsetse clearings and clearings made for agricultural purposes where it is proposed to break up the ground with ploughs. The object, in anti-tsetse clearings, is to destroy and keep suppressed in the cheapest way any vegetation which would harbour fly. From this view-point, whether stumps take a long time or short time to decay, whether they are present or not, is of no importance as long as regeneration is controlled. To make anti-tsetse clearings fit for the plough would entail considerable extra work and this would be reflected in much higher costs than the above."

(j) An experiment in task work as compared with day work.

It will not be out of place here to refer briefly to some experiments carried out by Napier-Bax (with Vane as a valuable assistant) designed to test the possibility of employing task-work methods as against day-work methods in making clearings with paid labour. A paper on the subject written by Napier-Bax and published in *Tropical Agriculture* (Napier-Bax, 1933) is quoted :—

" In the past, the gangs of comparatively raw native labourers have been worked on the ordinary day principle, the European Reclamation Assistant in charge, with his native staff, pushing the labour as hard as possible to obtain the maximum results within the limits of the hours of the day's work. This is referred to as ' day work.' Task work has never been adopted by us to any extent owing to what was considered the insurmountable difficulty of assessing a fair day's work in bush of varying types. The density and nature of the bush vary not only from day to day as the gang progresses, but from hour to hour."

In task work, the employer pays the same remuneration as was paid for day work, on the understanding that on completion of the daily set task the

TABLE 62.

Comparison of results obtained by day work and task work respectively.

	Day work			Task work		
	Total number of sq. yards cleared	Area cleared per man per day. Sq. yards	Average number of hours worked per man per day	Total number of sq. yards cleared	Area cleared per man per day. Sq. yards	Average number of hours worked per man per day
Heavy bush. Temporary methods. (Mantine Hills clearing)	1,400,000	1,338	8	1,400,000	1,615	7 hrs. 31 min.
Heavy bush. Permanent methods. (Ngongho river clearing)	440,000	265	8	512,000	373	7 hrs. 15 min.
Very light bush. Permanent methods. (Seseku clearing)	2,690,700	1,040	8	6,459,300	1,857	6 hrs. 48 min.

BENEFITS OF TASK WORK.

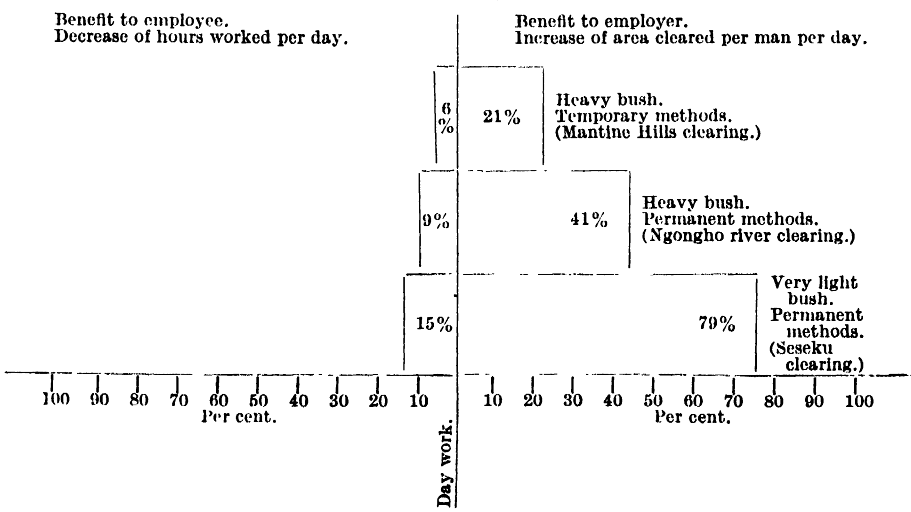


TABLE 63.

Savings in cost and time secured by adoption of task work.

Clearings	Cost, had whole clearing been made by day workers	Cost, had whole clearing been made by task workers	Saving on cost obtained by employment of task workers	Extra clearing which could have been done had savings obtained in col. 4 been employed on further clearing by task workers	Time, had whole clearing been made by day workers	Time, had whole clearing been made by task workers	Saving on time obtained by employment of task workers
	Shs.	Shs.	per cent.	per cent.	Days	Days	per cent.
Heavy bush. Temporary methods. (Mantine Hills clearing)	795/00	659/00	17	21	8·4	6·9	17
Heavy bush. Permanent methods. (Ngongho river clearing)	1,365/00	970/00	29	41	14·4	10·2	29
Very light bush. Permanent methods. (Seseku clearing)	3,345/00	1,872/00	44	79	35·2	19·7	44

Note 1.—The above figures are worked out on the basis of a constant gang composed of :—

Reclamation Assistant 1 at Shs. 13/- per diem	13*s.*
African Assistants 3 at Sh. 1/- each	3*s.*
Nyamparas 10 at -/40 each per diem	4*s.*
Labourers 250 at -/30 each per diem	75*s.*
Total . . . . Shs.	95*s.* per diem.

Note 2.—All days represent a full working day, *i.e.*, 8 hours in the case of the day workers, and in the case of the task workers the time taken to complete the task.

labour is free to return to its camp. The employer hopes to gain more work for the same remuneration even though the hours be shorter, while the shorter hours of work are the incentive offered to the employee.

The objects of the experiments are therefore :—to find out (i) whether the principle of task work can be applied to a gang of 150 to 350 men in the field making anti-tsetse clearings and (ii) whether, with equal remuneration, more work is done by task workers than day workers.

Regarding the laying out of the task work, Napier-Bax wrote :—

" In the morning, after the labour had been started on its day's work, the Reclamation Assistant proceeded to lay out the tasks for the next day. The area demarcated for each section depended wholly on the ease or difficulty of clearing that particular type of bush. The task was marked out with the help of a prismatic compass and blazing the trees. Paths were not cut between each task."

TABLE 64.

Trees and thicket units on one acre.

Composition of bush	Heavy bush. Temporary methods. (Mantine Hills clearing)		Heavy bush. Permanent methods. (Ngongho river clearing)		Very light bush. Permanent methods. (Seseku clearing)	
	No. of units in day work section	No. of units in task work section	No. of units in day work section	No. of units in task work section	No. of units in day work section	No. of units in task work section
1. Trees.						
(*a*) Hard-wooded.						
36 inches in circumference and over	5·9	5·5	2·6	3·8	0·9	1·2
27 to 36 inches in circumference	4·5	5·5	3·0	5·0	0·3	1·1
18 to 27 do. do.	9·8	13·1	10·4	9·2	0·5	3·2
Under 18 do. do.	28·4	56·0	39·6	36 5	18·1	13·5
(*b*) Soft-wooded.						
36 inches in circumference and over	1·4	2·6	3·0	3·5	0·0	0·0
27 to 36 inches in circumference	3·4	7·6	5·7	5·4	0·0	0·0
18 to 27 do. do.	12·8	23·4	20·4	23·1	0·0	0·0
Under 18 do. do.	86·4	66·0	46·5	54·2	2·2	0·9
2. Thicket units.						
72 inches in circumference and over	5·2	10·9	9·1	13·1	1·7	1·6
36 to 72 inches in circumference	15·7	17·4	13·0	16·5	4·4	6·0
18 to 36 do. do.	14·5	17·9	24·3	12·7	7·8	10·1
Total	188·0	225 9	177·6	183·0	35·9	37·6

N.B.—All measurements were taken six inches above ground-level, and in the case of thicket units, taken around the clump, to include the many stems of each unit. Thicket units under 18 inches in circumference have been omitted.

The foregoing conclusions may be summarised as follows :—

" The principle of task work was found to be applicable in the field even for such varying bush as is daily encountered in making anti-tsetse clearings. The Reclamation Assistant found no difficulty, after a comparatively short experience of day work, in assessing a fair task for each section.

" In three typical clearings, ranging from virgin bush to the cleaning up of an old and badly made clearing, better results were consistently obtained with task-work methods.

" More spectacular results were obtained in the cleaning up of an old clearing, less so in virgin bush.

"The Reclamation Assistant preferred task work to day work.

"Task work was more popular with the labour than day work, but it was always necessary to guard against making the tasks too large.

"The quality of the work did not deteriorate when the labour was employed on task work." (Napier-Bax.)

(k) Mechanical clearing.

Thicket cutting is a laborious task when carried out by hand with a cutlass, for the whippy stems tend to yield and avoid being cut and the spreading branches near the ground make it difficult for the natives to get at them. Enormous areas of the "Mallee scrub" in Australia have been destroyed by the use of rollers drawn by horses and motor traction, and when I visited the United States in 1927 the Forestry Department there had begun to use Holt tractors to destroy the dense scrub in intended fire-breaks by smashing it down. Tanks had been suggested and they certainly smash up thoroughly the vegetation they pass over, but the expert officers at the War Offices both in London and Washington were consulted in conversation and it was concluded that the cost would be prohibitive.

Our 6-wheeler Guy lorry was purchased originally partly with a view to carrying out experiments on the above lines in the destruction of the scattered thickets that were serving as breeding-places and refuges. A lorry rather than a heavy tractor was chosen as being more likely to be useful to the Department for other purposes if the experiments failed. Actually it has been in use for these purposes for the past six years and has been invaluable, carrying as it does quadruple the load of a Chevrolet lorry at an expenditure of double the petrol. It may be added that the Guy lorry was chosen as one which had already been shown to be cheaply and successfully convertible to running on producer gas.

Three experiments against thicket have been carried out with it. In the first of these, against a close, full-grown stand of *Dichrostachys glomerata* and *Combretum purpureiflorum*, it was very successful, despite a hopeless form of saw and a bent-down saw carriage. Here visibility was sufficiently good to enable the driver to attack the stems at effective angles. In the second experiment against a much leafier and more tangled form of thicket in long grass, with visibility nil and the saw-nose bent to the ground through a resulting accident, it was unsuccessful. In the third experiment, against similar thicket in the leafless period and with the grass short, it once again did quite well. The saw also easily cut through 8-inch stems of *Commiphora*. It should rapidly clear the hard-pan patches on which this tree and *Lannea* grow and that are the concentrating places of *G. swynnertoni*. This saw, however, was in any case intended only as the first piece of mechanism to be tried. Rollers (as in Australia), graders (as in America) or some other tool might replace the saw, and we have experimented with rollers drawn by tractors. What may be the actual ultimate tool was led up to by a suggestion by Messrs. Napier-Bax and Vicars-Harris, that a circular saw might be driven pneumatically from the lorry. This was modified by Mr. Eraut, Chief Engineer to the Crown Agents, who suggested a pneumatically operated secateur on an arm. This was made for us by the Globe Pneumatic Company in London and its manager, Mr. Hill, with the writer, tried it out in a strong holly thicket in the New Forest for the use of which for the experiment permission had been obtained from the Deputy Surveyor in charge (Mr. Young). It cut stems up to 2½ inches like cheese and is expected by Mr. Hill, in a larger size, to cut stems of 5 or 6 inches.

2.—THE TECHNIQUE OF GRASS-FIRE CONTROL.

Prior to the burning season two parallel lines of fire-traces are made round the area to be preserved, and, when the grass is ready, the space between the traces is burned. The fire-breaks thus formed are not less than 100 yards broad. On two occasions a fire has leaped a fire-break of this width, once through a whirlwind, once through the carriage of burning material by a strong wind. The natives everywhere are warned not to burn, both through their chief and ourselves, and the warning is repeated from time to time.

A native watchman is stationed on a great rock on Old Shinyanga kopje throughout the day. On detecting smoke anywhere he at once cycles to the station a few hundred yards away, gives the alarm and states the locality. A "fire-card" which constitutes its holder the fire-officer for the day, is in the hands of a European of the staff at the station; he may not leave the latter without arranging for someone else to take the fire-card. At the boma * are always kept a 50 gallon drum of water and a number of petrol tins (for supplying the fire-fighters with much needed drinking water) as well as pangas (bush-cutlasses) for cutting down branches for beating out fire. At least one lorry is always on hand in the fire season.

On the alarm being given to the fire-officer, the latter loads up the tins, pangas and as many men as can be collected and drives to the scene of the fire. All officers handling gangs in the bush have standing orders to drop work and go with their gang to the scene of any fire that is detected in their general area. If necessary villagers near the fire are called out; they are paid for their assistance. The fire is beaten out.

Every effort is made to trace the lighter of the fire and he is charged before the Chief, tried and, if convicted, punished by the latter.

3.—WATER SUPPLY : THE MAKING OF A COFFER-DAM, AN EARTH-TANK AND A ROCK-CATCHMENT TANK.

(a) The coffer-dam.

(pl. 16, fig. 3.)

Water-holes in the bed of a sandstream are usually found where a reef of rock runs across the latter and prevents the further flow downward of the water seeping under the sand when the main river dries up. The coffer-dam is on exactly this principle. A piece of the river is chosen with clay or rock bottom and long beds of sand up-stream, and a masonry wall is built across at this point. It is based on the clay or rock below and its shoulders go well into the banks. Its top projects but slightly above the sand and, actually, a wall of stamped clay between relatively slight stone walls or even without them would do as well. An adjunct which the natives often, however, neglect, scooping instead their holes in the sand as of yore, is a sump or well above the cross wall (*see* illustration). In building this sump narrow openings are left between the vertical sides of the stones that compose it, large stones are piled loosely around it and, outside these, smaller and smaller stones and finally sand. The water thus filters in without sand. A wooden cover can be bolted on to its top in the rains to keep it from filling up.

It is important in choosing the site for a coffer-dam to make sure that the underground seepage is flowing in the present bed of the river. Sometimes this underground dry-season stream still follows the deep-buried sands of an old river-course that deviates from that of the modern river in the rains.

* *See* Frontispiece.

(b) The earth-tank.

As the new areas have been opened up, the problem of an adequate water supply has demanded attention. Particularly has this been so in the Huruhuru where many thousands of cattle are now grazing. Pl. 16, fig. 1, illustrates our original form of tank. This has been modified and improved. The tanks we are now making to fill the want consist of two main excavations of this type with a cattle-watering tank behind. The two main reservoirs are fenced off from livestock to save the water from pollution and prevent cattle breaking down the bank. The watering tank situated behind them is provided with a ramp and troughing for cattle and is fed from the main reservoirs by pipe lines fitted with cocks. During the first storms of the wet season all three excavations fill to the brim and as the water is used refill at the next storm. On the approach of the dry season the watering tank is first drunk dry and the troughs exposed. Then water is drawn from the first reservoir and stock watered at the troughs. This is a better method than filling the watering tank to the brim again which would only increase loss from seepage and evaporation. In the course of time the first reservoir empties and the opportunity is taken of cleaning it out before the onset of the next rains. Meanwhile the second reservoir is drawn upon and if judgment is exercised the water will last until the wet season. In this way a continuous supply of water is assured for settlers and their cattle and each reservoir can be cleaned every alternate year. Each main reservoir is designed to hold half a million gallons and the watering tank 200,000 gallons —a total of 1,200,000 gallons. This should suffice 2,000 cattle for the 5 months of the dry season and five times as many during the rains. It takes 1,200 tribal labourers 10 days to make a tank of this sort.

Single tanks of a shallower type intended solely to carry the cattle over the drier spells of the wet season are also made. These make possible the rotational grazing schemes of the mbuga systems.

(c) The utilisation of rock catchments.

Large granite rocks, like roofs, catch an immense quantity of water in the course of the rains and this water is always capable of being guided into a tank. In Ndode (pl. 16, fig. 2) we had a natural tank to our hand. It was filled to the brim with soil and decomposed rock, but, on digging out this large mass of material, we found, as we fully expected, that the great hole left was water-holding, being probably simply a cavity eaten out of the rock by the action of humic acid in water, like so many holes of much smaller size that are everywhere to be seen on such rocks. Cement walls a few inches high only were run round the outside of the rock in such manner as to guide the rain that fell on it into the tank. In the case of an ordinary rock surface, without a natural tank, the latter would be constructed with stones and cement at the base of the rock and these guiding cement walls sloped into it. If the soil at the foot of the rock were good clay, only an excavation and no cement walls would be necessary.

Ndode holds 200,000 gallons. Its potential capacity is 500,000 gallons if the catchment could be increased.

PART 7.—DEFENCE AGAINST FLY ADVANCES.

A.—THE ADVANCE WESTWARD AND SOUTHWARD OF THE *MORSITANS* BELT IN WESTERN KONDOA, CENTRAL PROVINCE.

Jackson, who was stationed first at Sambala, and then at Masiliwa, both points to which this fly belt had successively advanced, has watched the advance closely for some years and the passages following that are in inverted commas are quoted direct from his account of it (Jackson, 1933*d*). Map 5 should be referred to for the localities mentioned.

1.—THE HISTORY OF THE ADVANCE.

G. morsitans seems to have been on the upper Bubu since before the war, for our troops advancing on Kondoa–Irangi from Hanang " sent their animals through the upper Bubu country by night in order to minimise loss by fly." An odd fly only was then reaching the Kondoa–Singida road and one taken there in 1914 is stated to have caused much surprise to the German Veterinary Officer.

(a) The advance north of the Kondoa–Singida road.

Jackson was shown abandoned cattle settlements between the upper Bubu and Sambala, and Sambala and the " Mangati " plains to its north. The flies reached Sambala in about 1918 and Umu, well north of the road and far west of Sambala (*see* map 5), in 1927 or 1928.

" On the 8th of September, 1927, Mr. Potts, passing along the road by car from west to east, took a few fly between Masiliwa and the Malulu river. On the 5th October, 1928, the writer, going by car from Kisima cha Mungu hill to Masiliwa, saw no fly from Kisima cha Mungu to the Malulu river and then took six individuals between there and Masiliwa. Mr. Ruhl, who took two flies on this section of the road in 1928, states that fly were already thick on the Malulu river north of the road. Evidently fly did not spread along the road from points crossed earlier to the east, but first invaded the country west of Sambala, and then descended on the road from the north." Masiliwa was infested by 1928 and the flies had reached the Rift valley west of it by the middle of 1934.

(b) The advance south of the road.

Flies already occurred not far down the Saranda road in 1920, " but they were not in sufficient density to prevent the use of ox transport."

" In 1926 Messrs. Potts and Burtt started investigations in this part of the area. They found heavy concentration of fly about Selya Lake and on the Saranda road, and the southern boundary had been carried forward as far as Tsantsai village and Githlau hill, but not to the villages of Songa and Klankase. The Director of Tsetse Research instituted clearing measures followed by settlement at Selya, and reduced the numbers of tsetse to the west of that area by other means."

" In October 1928 Captain V. A. C. Findlay, Field Experiment Officer, Department of Tsetse Research, carried out a survey of the fly boundary

south of the Kondoa–Singida road. Dr. T. A. M. Nash, Entomologist, Department of Tsetse Research, had also made certain observations in the Jogose valley area in 1927–28; other reconnaissances were carried out by Mr. Potts there about the same time, and the writer made more detailed observations about the head of the advance in the Jogose–Rungurunguse–Kirambo–Mataka–Kiguru area in 1928."

The position in 1928 and at previous and subsequent dates are shown by successive lines on map 5.

2.—EXAMPLES OF THE GREAT INCREASES IN FLY DENSITY DURING THE ADVANCE.

" The great increase in fly density on the road from Masiliwa to the Malulu river has been remarked above. In other places striking increases also occurred, some examples of which are given below.

" *Path from Mataku village to Kopase village.*
31.5.28, 1 fly, and 1 seen. None on return journey.
6.12.31, 48 flies (1 journey).

" *Path from Mataku village to Kiguru village.*
6.9.28, 1 fly, near Mataku. None on outward journey.
3.12.31, 19 flies (1 journey).

" *Path from Kiguru village to Maji-Malulu village.*
6.9.28, none (2 journeys).
3.12.31, 30 flies (1 journey).

" *Jogose-Thamba–Kondowa–Kirambo area.*
Fly about 10 times as abundant in December 1931 and May 1932 as from December 1927 to October 1928.

" From April to October 1928 the writer observed by regular fly rounds the spread of the fly westward in the Rungurunguse–Mataku–Kirambo valley area, all of which had remained practically or completely fly-free until after the rounds were begun. Similarly over a series of visits the spread of fly was observed from Munge hill and Muporu village to the Hanse swamp to the south."

" From the above detailed evidence there can be no doubt that a spread of fly has occurred from some point in the north-east of the area, probably mainly or entirely in the present century, and that this spread has continued to a depth of some 50 miles."

3.—FACTORS FAVOURING OR RETARDING THE ADVANCE.

(a) Climatic factors.

" Consideration of the recent history of the advance shows that it must have been particularly rapid in the three years from 1928 to 1931. Questioning of numerous natives in the lately-infested areas has produced the statement that marked increase and advance of fly took place following on the abnormally heavy rains of 1929–30. Visits to the eastern parts of the area in October 1930 confirmed this view. This is of some interest, since following on the heavy rains of that year Dr. Nash and other workers in the low-lying eastern Kondoa fly belt bordering the Masai steppe had noticed a great reduction in numbers of fly, together with a withdrawal of tsetse from the extreme south end of this fly belt. Mr. Potts has suggested that the two fly belts may repre-

sent respectively the dry-country and wet-country limits of distribution of *G. morsitans* and that a very wet year might therefore benefit the one and tend to destroy the other. From instrumental readings it is known that the western Kondoa–eastern Singida fly belt occupies in fact drier country than that in eastern Kondoa."

(b) Vegetational factors.

"Although, as will be seen in the next section, it would appear that the flies in the van prefer to follow the drainage lines, which implies that the presence of numerous small valleys running in the right direction might tend to favour rapid advance, it would appear that where suitable 'miombo' woodland occurs the advance will continue. If the 'miombo' is rendered more dense by discontinuous thicket, it seems less favourable as a fly habitat, especially in the rains when the thicket is in leaf. This is apparent from the following fly figures obtained near Masiliwa in 1931–32.

TABLE 65.

Effect on the density of *G. morsitans* of the presence of discontinuous thicket in miombo wooding.

Type of miombo	Length in yards	Mid dry season, 25 days		Rains and early dry season, 38 days	
		Total	Fly per day-yard	Total	Fly per day-yard
More open . .	1,200	584	0·0195	878	0·0193
More thicketed . .	400	86	0·0086	89	0·0058

"These figures show that in the dry season, when the trees and thicket shrubs are leafless or nearly leafless, flies are more than twice as common in the more open as in the more thicketed woodland; but that in the leafy season they are more than three times as common in the first type as they are in the second. Similar cases were noticed elsewhere."

Miombo re-growing on old cultivation seems relatively unfavourable to *G. morsitans* and its passage. "Dense, continuous thicket . . . appears, in sufficient width, to act as an absolute barrier to *G. morsitans*. . . . Well-defined paths through the thicket, whether of man or of elephants, greatly reduce the efficiency of the barrier, as of course do small islands of 'miombo' scattered through it.

"About Sambala in 1928–29 it was noticed that in large areas of *Acacia rovumae* bush and *A. Kirkii* fly was exceedingly scarce. Such an area occurred immediately south of Sambala and stretched from the open swamp of Nafimu north-east of Swagaswaga hill to some miles north-west of Kisima cha Mungu hill on the Kondoa–Singida road. Consequently there was a long delay before the 'miombo' woodland west of Kisima cha Mungu became infested by fly."

(c) The game factor.

"From what has been said above it is evident that game, the food of the fly, is common throughout the area. As there is no question of wholesale migrations of the animals to and fro, they can have had very little effect in assisting or retarding the advance. Moreover, from experiments described elsewhere it is known that flies will travel independently upwards of a mile in a

few hours; and, since the rate of advance of a fly belt is only two or three miles a year, the rôle of the game in carrying flies into uninfested country into which they would otherwise wander unaided must be quite negligible.

"The importance of the game might lie in carrying the fly across some barrier through which it would be unwilling to venture of its own accord."

(d) The population factor.

"While small villages (*e.g.* Lankasese) are often associated with a very dense tsetse population, it usually happens that fly is rather scarce about larger settlements, such as Masiliwa and the settlements along the east side of the Bubu valley. The writer does not believe that this is by any means entirely due to disturbance of the game animals in the neighbourhood of large settlements or to alteration of the surrounding woodland, and considers that more work on this problem is necessary before a satisfactory explanation can be found. Meanwhile it is worth remembering that a settled barrier backed by thicket may perhaps be the best of all practical defences against the advance of fly." [*See* p. 325 above.—C.F.M.S.]

(e) Roads.

"It has already been noticed that the fly advance crossed the Kondoa–Singida road at three points, and did not proceed along it. As with the game animals, it would not seem that a road assists the fly advance unless it crosses some barrier unfavourable to the fly.

"It is interesting that flies are continually being carried through the Mnangana thicket on lorries and cars passing along the Kondoa–Singida road. They are picked up in very large numbers (hundreds at a time) on the road east of Masiliwa, and have been carried as far as Mgori's village in the Rift valley, 10 miles west of the thicket. Yet fly has not yet established itself anywhere in the apparently suitable country west of the Mnangana thicket, and cattle in the settlement of Lamba remain healthy. At the same time, fly are advancing round the north and south flanks of this thicket, and the invasion of the Lamba area must, it seems, be only a matter of time." The same observation appears to apply to the road from Kondoa to Saranda.

(f) The mechanism of the advance.

"Except in certain special sites, the apparent density of flies in the drainage valleys is not much if at all greater than in the surrounding 'miombo.' But where fly is scarce, as at the fringe of an advancing fly belt, it seems that flies are relatively numerous in the drainage valleys and scarce in the 'miombo' between them; moreover flies [in such a situation] are not hungrier in the drainage valleys than in the 'miombo.'

"Thus from a number of extensive reconnaissances carried out in scarce-fly areas north and south of Masiliwa in 1931–32, the apparent density of fly in the drainage valleys was about four times as great as that in the 'miombo' woodland, where flies appeared equally hungry.

"In nine days' observations made from November to February, a fly round carried out at Masiliwa showed a total of 78 flies in a narrow drainage valley on a transect 1 mile in length and 15 only on a transect of equal length in the 'miombo' woodland alongside. The percentage of females was 13 in the 'miombo' and 23 in the valley; but an analysis of the hunger condition of the mature male flies from the two transects showed that those from the

valley were scarcely hungrier than those from the 'miombo.' This is a fair instance of the 'scarce-fly' type of distribution commonly observed about the head of the fly advance.

"Apart from this question of social concentrations in the valleys, the advance may be supposed to proceed somewhat as follows. From the dense fly population behind, where breeding occurs, flies are continually wandering forward to a depth of several miles in accordance with what is known of the independent movements of tsetse flies. (One fly marked near Masiliwa was recaught in the Kitalala hills, 20 miles to the south-east; and two flies marked near Masiliwa were caught at Duwa Mganga, 8 miles to the south.) Among these wandering flies composing the advanced fringe of the belt, perhaps to a depth of 6 miles, a greater number probably die without breeding there, the flies being too thinly scattered for many meetings between the sexes to occur. Thus it is the increase of the main body and not the 'scouts' ahead which in the main determines the speed of the advance."

The greater the density in the main body the more numerous must be the advanced flies, and the greater, therefore, the chances of their meeting.

4.—SUMMARY.

"An advance of tsetse flies (*Glossina morsitans*) has taken place in Kondoa, Mbulu, and Singida Districts of the Central Province of Tanganyika Territory to a maximum depth of about 50 miles from its origin in northern Kondoa. . . .

"Factors influencing the rate of the advance are discussed. Wet years in dry country such as that under consideration may favour the increase of fly. Suitable 'miombo' woodland implies that the advance will continue more or less rapidly; more thicketed or stunted 'miombo' is less favourable. Dense, continuous thicket is an absolute barrier where it occurs in sufficient width. Certain types of thorn woodland, if extensive, delay the advance, and may stop it. The movements of animals and the presence of motor roads do not appear to have any effect on the advance as long as it is continuing through suitable country. The presence of large settlements is associated with a lower apparent density of tsetse in their neighbourhood. Dense, continuous settlement is a barrier to fly.

"It would appear, but is not proved, that flies when still in small numbers tend to keep to the drainage valleys which under other conditions are used purely as feeding grounds. It is suggested that they may do this for social reasons. The progress of the advance is thought to depend mainly on the increase of population of tsetse behind; this is because a larger population will provide a larger number of flies wandering ahead of their own accord, not because there is any congestion behind. It was not determined whether the most advanced flies have any tendency to return to the main body."

As stated by Jackson in a quotation above, one attack was made by us on this fly advance in 1927 while it was still not very far advanced. It is possible that, if pressed, this attack might have succeeded. A still better opportunity occurred later when the flies were approaching the thicket system Mnangana–Songoro–Kutsuwa (*see* map 5), and yet a further chance was offered on the line Gindaro–Madanda–Boro–Takwa–Manyigi. Unluckily these chances coincided with the recent financial depression, or as stated elsewhere, we might have learned how to stop an advance of *G. morsitans* without sheer clearing and settlement. An opportunity for cheap work that may never recur was missed.

5.—THE PRESENT POSITION.

The flies have reached the Rift valley westward from near Mgori's right down to Manyigi and have even surmounted the rift wall. Southward they have outflanked the Madanda thicket, passed Kindo and are pushing to Boro. All chance of stopping them here with the aid of the thicket systems is ended, and a stand is being made in the last ditch of all by native clearings devised merely to protect the Usandawe headquarters. The latest news from the east flank is that the advance has crossed the Kondoa–Dodoma road south of Kondoa.

6.—LATEST RECOMMENDATIONS.

Burtt wrote following an air reconnaissance over the area in November 1933 : " It appears from all present evidence that there has been a big fly advance southward in the past year and according to the District Officer the fly is so much past the boundary of the reclamation scheme put up by Jackson, 18 months ago, that it is now impossible to put this scheme into practice—moreover they say that fly is now very common at Kindo and therefore presumably well on its way to Lalta—they also say that fly is across the Mkenke and half an hour's walk from Kwamtoro. None of these things has been verified by the Tsetse Research Department and therefore I have been loath to form any opinion from our flight over Usandawe, without previous accurate ground evidence. I therefore merely showed the District Officer the easiest line to clear along the very open country between the settlements of Kwamtoro and the Mkenke Mbuga which prolongs itself northwards up the Handa valley past Laoda and Kindo, and the clearing up of the country between Kwamtoro and the Duyu settlements, linking them up with Lalta. From the air it looks as if fly can easily sweep down from the north-west and hit the Lalta country in the back. So any clearing that is done will have to be consolidation of grazing and cultivation in the easiest clearable areas, namely those mentioned above."

That is to say, the Wasandawe, mainly a cattle-keeping tribe, have lost the bulk of their country and are losing most of the rest of it. The next stand, when Kwamtoro and its new clearings are passed, might be on a narrow front on the Bubu, to prevent the infestation of north-west Dodoma. The measures being taken for the protection of eastern Singida from this advance are stated on p. 434 below.

B.—THE HIKA FLY ADVANCE, CENTRAL PROVINCE.

(map 6.)

Climbing the successive shelves of the Rift Wall in the train as one approaches Manyoni from the east, one notes at Saranda station a scarp, rising from the *Acacia spirocarpa* bush beside the line, that is clothed on its top with miombo. This is the edge of the miombo area that is bounded on the east by the great thickets of the Mponde river, largely below the Rift Wall, and on the west by the yet greater thicket that lies between Manyoni and Kazikazi. Northward the miombo runs towards the cultivation steppes round Singida itself and, on the Rift top, nearly to the Kondoa–Singida road.

J. F. Gabbutt, then Tsetse Reclamation Officer, now Game Ranger, reconnoitring this area in 1927, reported flies in the neighbourhood of Hika, which lies in the southern end of this miombo area. Burtt, sent to investigate from the air, made three flights over the area in August and (again) November 1931

and ascertained the distribution of the vegetation (*see* map 6). Examining the situation thoroughly on foot as well, he established that the flies were *G. morsitans*, that the fly belt was of recent origin, that the area covered by them was about 200 square miles and that " the densest fly are to be found in a triangular area extending about three miles N.N.E. and N.N.W. of Saranda along the top of the scarp and some two miles N.N.W. of Irola village. A party traversing this triangle captured 108 flies in one hour, there being two catchers, one of whom was not very efficient."

1.—VEGETATION.

This is mainly miombo (*Isoberlinia-Brachystegia*) part of which (as near Hika) contains an unusual number of small thickets, though elsewhere, where it is more open, the flies were much more abundant.* Gall-acacia mbugas are present, as are riverine stands of the spectacular feather palm *Hyphaene Bussei*. The better streams (Hika and Ruwiri) are lined also with thick fringing forest, partly of *Piptadenia Hildebrandtii*, with *Acacia usambarensis*, *Tamarindus indica* and other large trees, and groves of *Acacia Kirkii* and *A. Stuhlmannii* are present. Those of the first species are a special feature between Saranda and Irola.

2.—GAME.

Elephants are rare visitors to the plateau, but a small herd works from Kilimatinde up into the miombo woods in the dry season. But " the quantity of rhinoceros tracks in the Saranda Hika area is phenomenal. These animals frequent the *Commiphora–Acacia* semi-mbuga thickets tunnelling pathways through the thick Acanthaceous scrub, which they eat. They are very fond of the thick *Acalypha–Justicia* thickets clothing the escarpments, while the small *Pseudoprosopis Fischeri* thickets on the summit of the scarp are much tunnelled by these animals. . . . In the dry season the rhino concentrate in the neighbourhood of the permanent waters. With the first heavy rains they disappear with remarkable suddenness to other feeding-grounds, only a few remaining in the area; they are alleged to migrate towards the Sandawe country. During our reconnaissance flies were captured in thicketed bush inhabited by these animals. Zebra, eland, giraffe, waterbuck, greater and lesser kudu, duiker and dikdik are resident in the area but become much commoner and more concentrated in the dry season. Fresh eland, giraffe and zebra spoor was seen on the brow of the scarp overlooking the railway above Saranda. Bush-pig spoor was frequently seen, while wart-hog are alleged to be common by the natives, though none were actually seen. Baboons and [so-called] Sykes's monkeys (*Cercopithecus leucampyx*) are common in the riverine forest and along the cliffs of the Saranda scarp."

3.—APPARENT ORIGIN OF THE FLY BELT.

It is known that there is no tsetse west of the Singida–Manyoni motor road till one arrives beyond the great thicket. Also that from a few miles south of the railway at Saranda there is no tsetse till the Kisigo river is crossed. Investigation of the possibility that the flies had been carried to Saranda on lorries on the Kondoa–Saranda road, latterly heavily infested below its junction with the Kondoa–Singida road, seemed to negative this possibility. Burtt's tentative conclusion ran as follows :—The scarp above Saranda bears a strong similarity to the Kikore scarp which is known to be specially favourable to

* See extract from Jackson's note given on p. 426 above.

G. morsitans, for, packed with breeding-places, clothed with the favourite miombo and carrying a game population (at Saranda eland, giraffe, zebra, bush-pig and wart-hog) it harbours a great density of fly. The trains, passing through the Itigi thicket barrier from Kazikazi on the west, are continually carrying the flies. " During years of fly transport thus to Saranda there may have been many years of failure to become established and breed," but, ultimately, " the flies found an optimum of meteorological and biotic conditions one year, perhaps about 1925, and succeeded in establishing a colony.

" The development of this little fly colony took place in a little frequented area, the natives passing through would not recognise the strange insect as a scourge, as even to-day many of the local natives do not recognise the fly and continue to graze their cattle in it, so that it is possible that the colony was able to gather strength unnoticed until to-day it has developed into a serious problem and is sweeping like a fire into the tracts of miombo north and west " (Burtt, report).

C.—THE ADVANCE ON SINGIDA, CENTRAL PROVINCE, FROM THE SOUTH-WEST.

The enormous western belt of *G. morsitans*, occupying about 90,000 square miles, had been held up in its eastward advance by the great thicket system of Itigi (*see* map 6 and pl. 17, fig. 1). In 1926 the flies had already begun to appear on the Singida side of it, in the north. In 1927 we were called in by the District Officer to guide an attempt at defence. We found that a narrow clearing had already been made, but, as it ran in the direction of the fly advance instead of across it, it was a very great deal worse than useless, for the flies apparently go forward first along open margins and were utilising it thus in aid of their advance.

Burtt, who had gained much experience already of tsetses and had supervised quite large operations in three different districts with success and with praise from the Administrative Officers concerned, was entrusted with the work. Time was short, but he carried out a survey which exactly hit off the situation and I myself, going over the ground with him, confirmed the plan of defence.

The general position was that the flies were already present in density against the general thicket barrier, and the plan was to carry out a clearing which should extend from Matalele northward into the Iwumbu mbuga, with such widening of this as should be necessary to prevent outflanking of the thickets. The clearing in question would incidentally close the gap between the thicket patch north of Matalele and the main thicket (*see* map 6) and reinforce the former, as the densest fly population was up against this, and its composition and width were not regarded as sufficient by themselves to withstand the probable infiltration. It was also proposed to stop a narrow opening, 300 yards broad, a little further south in the thicket. An odd fly was found already on the wrong side of the barrier up to a total depth of twelve miles, but the concentrations which these advanced flies were beginning to form were still very few and small (and were located by Burtt) and there can be little doubt, on all our experience, that with these concentration points destroyed (as Burtt very effectively destroyed one) and reinforcement excluded, the " odd fly " would not have successfully colonised the area incipiently invaded.

As there has been misapprehension over the relative failure of the initial attack made on the position it is well to state briefly the facts of the case.

When I arrived at Singida, I was informed by the Assistant Administrative Officer present on information from the Chief (the latter informing me also) that all was ready and the people could come out at once. They came out in four successive relays. Food was ample, for, though a number of the men did not bring their food, a reserve of many tons had been laid in. Water was also ample, for the Director of Geological Survey was with us and, with his help, abundant water was located and several fine wells were available before the river-pools gave out. The supervision was good, for Burtt with a history of success was in charge, I assisted at the start, and the subordinate European supervision on normal standards was ample. The Chief was present also and, for part of the time, an Administrative Officer.

After devoting a fifth of the labour to the building of villages (at the instance of the Administration), and diverting the necessary number to water supply, carrying of stones for wells, carrying of water and some necessary road-making, 6,450 men were left for the clearing, including the cooks for the whole of the work. 2,750 cleared great pieces of riverine forest which harboured elephant and buffalo and, in the roads of the latter which everywhere cut up the forest, much tsetse. This work was exceptionally heavy—certainly ten times heavier than ordinary savanna clearing—and was done very thoroughly. The remaining 3,700, out of the total of 9,928, were those who disgraced themselves by clearing in ten days only 1·2 square miles of ordinary savanna wooding, in addition to three miles of light ring-barking to join up with the Iwumbu mbuga.

The clearers of the riverine forest were Jumbe Sima's men. They had evidently a popular chief and worked splendidly. The 3,700, on the other hand, behaved like Mwanasali's men in Nzega. Their chief, or a supervisor, or myself, had only to move off a few paces, back turned—not going away—and the work, none too good with us watching, ceased at once. Numbers of palm-fruits were obtainable in the long grass by the river, and natives would at all times be found lying there sucking them. There was no hunger or thirst, little breakage of axes as yet, no lack of meat or of friendliness or any visible discontent at all. Innate lethargy or pleasantly passive resistance was the impression conveyed. The District Officer had told me that lethargy was the tribe's characteristic and that labour recruiters normally avoided Wenyaturu. "You are dealing," he wrote to me during the clearing, referring to food and work, "with a most improvident and lackadaisical tribe, and I'm afraid it must be taken as part of the trials of the job." Further it was not considered that in the circumstances any example could be made *pour encourager les autres.* The lethargy was particularly strong in the headmen, who should have been encouraging their men.

The above, with the miserable axes, which broke wholesale, no others being yet available, was the main reason for the small work done in the savanna. Sima's work on the heavy forest actually broke the back of the whole work to be done, so that, had the defence been continued in subsequent years, such light work only was left that, with good propaganda such as we used in Shinyanga and the good axes which later were obtainable, the whole clearing could have been pushed through, even if at a greater expenditure of labour than is usual in the Lake Province, and the fly advance (I believe firmly) stopped.

The position both in 1927 and in 1934 is well shown in map 6. In the interval the tsetse, advancing at an average rate of four miles a year, outflanked our defensive thicket, closely approached the cultivation steppe of

Singida and threatened south Mkalama. Flights by Burtt, and by myself with Burtt, in 1932, showed that there was nothing, unless sheer clearing, that, so far as could be seen, would prevent the flies from penetrating far into Mkalama in addition to eating up Singida. The measures being taken now will be dealt with in subsection E.

D.—THE ADVANCE INTO NORTH-EASTERN SINGIDA, CENTRAL PROVINCE.

The great " Barabaig " belt of *G. swynnertoni* which fills the Yaida depression, extends from Mount Oldeani to west of Lake Basotu and Basodesh and will be mentioned in more detail under subsection E below, has at its south-western corner approached close to the border of Singida. Here the thorn-bush which the flies are infesting narrows into a neck a dozen miles wide between the main open cultivation steppe of Mkalama at the Iambi Mission and the Dulumo river and the main cultivation steppe of Singida at its north-eastern point in Wilwana. The flies were estimated to have been approaching this neck from the north-east at the rate of a mile a year and the neck itself, as representing the waist of an hour-glass, was chosen as a site for a defensive barrier by Dr. Armstrong and Mr. Currie. Jackson, Bax and myself were called into consultation. A view that the flies were through already was not supported by search by Jackson, but it is certain that the particular species concerned would readily cross the clearing were it still covered with fallen trees, just as happened in the early clearings in Shinyanga.

The present position is that the clearing—which is fortunately easy work—is still in prospect and that the flies have been reported as advancing at an accelerated rate. Actually, were the money we are asking for available, this would be a spot at which to carry out an experimental defence, which, irrespective of clearing and settlement, would probably be a success. The bush is like that of Shinyanga.

E.—THE POSITION AND MEASURES IN SINGIDA GENERALLY.

1.—THE POSITION IN 1934.

(map 6.)

By 1934 no less than four advances by the tsetse were converging closely on the cultivation steppe immediately surrounding Singida. There was the advance westward from West Kondoa which, as stated above, had already reached the Rift valley. There was the advance which had come through the gaps and round the head of the great thicket to the south-west in and after 1927 and which had devoured all the country between to the line shown on map 6. There was the Hika advance from the south which of late, however, had not come on as rapidly as was expected. All these were of *G. morsitans*, and there was an advance of *G. swynnertoni* coming in on the north-east from the Mkalama–Mbulu belt near Iambi. Four great armies had entered the district from all four points of the compass and already had occupied most of it.

For some years previously, when they were further away, it had been considered impossible or inadvisable to use tribal labour to stem these advances and we estimated, once they were through the thicket barriers, that to stop them with paid labour would cost £30,000. Now, however, sleeping sickness had broken out in Mkalama, the next district to the north, and the fear lest it

should invade Singida also was the incentive, pressed by the Sleeping Sickness Officer, for concentration of the outlying natives in the Singida District in settlements that should incidentally, if that were possible, form barriers against the fly.

Dr. Maclean calculated that the population of Singida, of 132,521 persons, could be contained in a hexagon, shown on map 6, which he caused to be marked out and which comprised 1600 square miles or one million acres. Five-sixths of the population was already living within it. The cattle population of the district was 245,000 head and the small stock 204,000. It was estimated that there were 100 square miles to clear and that from 18,000 to 20,000 men could be obtained for the work. In addition it was proposed to bring out the Wanyiramba of Mkalama to make a barrier from Sepuka to the Wembere that, if finished in time, should save the southern part of that district. The chiefs and people were now at last thoroughly alarmed at the loss of so much of their country and the present close proximity of the flies, and the Administration anticipated that successful tribal work would be possible.

Jackson was sent to Singida and made a fresh survey of the " fly." The lines on map 6, denoting the limits the tsetses had reached, are his, and the most advanced of them shows the position in May 1934. Mr. J. R. Curry, District Agricultural Officer, carried out a survey for Dr. Maclean from the agricultural and water view-point and the whole position was considered by an inter-departmental conference which met in Singida on May 31st. The conference was attended by the Provincial Commissioner, Central Province, the Director of Agriculture, the Director of Geological Survey, the Director of Veterinary Services, the Sleeping Sickness Officer, Dr. Maclean, and myself.

It was unanimously decided that the Singida concentration proposed by the Sleeping Sickness Officer should be carried out. Also that clearing work should be commenced at once, subject to the provision of £1,500, which was regarded as an immediate necessity. It was regarded also as essential that the following work should be carried out during 1934 :—

(*a*) On the eastern side, the clearing and settlement of a length of thirty-four miles of the Rift valley.

(*b*) On the west, the clearing of an angled line twenty-four miles long from Ussure in the Mkalama District to Minyuge in the Singida District, turning at Sepuka, this being part of the general defence from the Wembere Steppe to the southern part of Singida. Jackson urged a turn north-west from Ussure to get further away from the tsetse.

Each clearing was to be two miles wide. " Unless sufficiently wide barriers are cleared within three years the fly will be behind the proposed defences."

2.—MEASURES CARRIED OUT IN 1934.

The work was left in the hands of Dr. J. S. Armstrong, Medical Officer of Singida, who had done most of the preliminary work and (in the field) of Agricultural Surveyor White of the sleeping sickness organisation. European supervisors were provided and paid for from tribal funds and the Administration and Chiefs " brought out the tribe." 24,000 Singida natives came out and a length of 4½ miles was cleared in the Rift valley from the Manyigi swamp

northward. The Wanyiramba of Mkalama, who came out to a total of 16,000–17,000, did more—18½ square miles being cleared in the Usule-Sepuka strip—where areas of existent settlement and light bush favoured speed. Re-growth, however, is considerable—25-50 per cent. in the Rift and 60–70 per cent. elsewhere—but settlers are coming into the clearings.

Burtt flew over the hexagon in December 1933. He roughly mapped the vegetation distribution, but the one important point noted was that thicketed country, such as might be made into a barrier, extended across the ultimate path of the Hika advance on a line south of the Singida cultivation steppe.

3.—SUMMARY OF THE POSITION IN 1934.

The amount of country lost in Singida during the seven years past was in 1934 1,300 square miles; the amount of country still infestable was 1,200 square miles. The amount still infestable in Mkalama was 900 square miles. The flies in May of 1934 had *not more than* eleven miles to go from Kipampa to Ushola * in the barrier south of Mkalama, and the advance had been at the rate of four miles a year in the past—*i.e.* they would be at the barrier by the end of 1936 even without specially favourable seasons. On the east and west of Singida the flies were in 1934 nearly up to the proposed barrier line. It was now a race between the flies and the clearers and settlers with the odds very strongly on the flies—even in south Mkalama. If the attempt at settlement is successful, it will be fortunate that the fly on three of the fronts is *G. morsitans*, regarding which p. 325 above should be seen.†

F.—THE ADVANCE BY *G. SWYNNERTONI* ON LAKES BASODESH AND BASOTU IN THE COUNTRY OF THE BARABAIG, SOUTH MBULU, NORTHERN PROVINCE.

" The Barabaig (incorrectly called Mangati, Watataru, etc.) are the largest clan of the Nilo–Hamitic Tatoga, a tribe akin to the Masai. . . . They are semi-nomadic pastoralists, with a Masai-like contempt for agriculture or manual work of any sort, though they are a hardy, brave people. They number 9,600 and own 12,700 cattle and 20,000 small stock " (Bagshawe, 1931).

1.—THE VEGETATION OF THE AREA.

Their country above (*i.e.* west of) the Rift scarp is thorn-bush, *Acacia spirocarpa* being particularly prominent, though " stink-bark " (*usambarensis*) is also abundant and open mbugas, areas of *Commiphora Schimperi* and narrow, ill-drained strips of a gall-acacia, *A. malacocephala*, making a finer tree than most gall-acacias, are interspersed.

Towards the Rift Wall eastward the country becomes more open and, for a distance back from the Wall, thickets (on the section best known to me) are not abundant. Yet there is much country, as round Basotu itself, which seems ideal for *G. swynnertoni*. The Wall itself is scrubby and would conduct the flies down. In the Rift valley south of Hanang is a great area of *A. spirocarpa* and *Commiphora* which, though unthicketed, contains thicket substitutes in the form of individual low bushes and low, scrubby, young *A. spirocarpa*

* *See* map 6.

† This was written in 1935. In May 1936 the situation is that the flies from the east are over the scarp and that those from the south-west are on the edge of the clearing south of Mkalama on a front of five or six miles. The situation is, however, not yet lost.

that would probably harbour this fly and carry it eastward and southward, if it were later to descend the scarp.

2.—THE HISTORY OF THE TSETSE ADVANCE.

" The whole of the area was formerly settled and grazed over by the Barabaig as far as the Ndagulda river and the Mkalama boundary. . . . Fly first made its appearance in the vicinity of Endabash some twelve years ago and caused large losses of stock. Natives living in that area at once moved back to their present limits near Lake Basotu. Haidum and Maghan were next infested and later Mara to a lesser extent. Stock was moved back to the vicinity of Giyeda Mog which in turn has been evacuated as recently as three months ago. Two years after the original evacuation of Maghan a few natives returned there with their stock as apparently fly had disappeared, but it returned the following year and forced them to retire again. . . . At Kara Kowet and between that point and Endamasak the country was also completely evacuated a few years ago, and though a few stock owners return to graze their stock no permanent re-settlement has taken place. This particular area was settled mainly by Gismajong and Wambulu, being outside the Barabaig country, and it must formerly have been highly cultivated, but it is now rapidly reverting to dense bush. Between Kara Kowet–Mara and the Yaida river native settlement has hung on in spite of cattle losses, though at Kara Kowet and in its immediate vicinity cattle owners informed me that they intended evacuating. A conservative estimate of the country already abandoned owing to fly advance is some 350 square miles. A further area at present uninfested of at least 200 square miles west of the Rift Scarp is in danger should the fly advance further at the danger points between Basotu and Bassodesh. Should such an advance become a reality there is nothing to prevent infestation of all the country east of the Rift Scarp to and around Mt. Hanang, and as a result the disappearance of the Barabaig as a pastoral tribe. They would be restricted to the open plain country south of Basotu. This area of only some 150 square miles would only be sufficient for the grazing requirements of a very limited number of stock-owners. The greatest immediate danger lies in the possibility of an infestation on the two lakes which would deprive at least 80,000 head of stock of water during the dry season" (Gordon-Russell, report, 2.iv.32).

The flies (*G. swynnertoni*) have advanced actually nearly to the small lakes mentioned above, but within three or four miles of the lakes only very small numbers have been taken at any time of the year and their progress appears now to be slow. In fact the big infestation is in the depression behind, and the numbers thin out as one leaves it. *G. pallidipes* also occurs in high density in the depression. Typical of the situation in the depression is the fact that when on the Yaïda river and below it Gordon-Russell took great numbers of pupae in every suitable breeding-site.

Clearings in the form of cutting out *spirocarpa* strips in " lean-and-fat " alternations of that type of wooding with open mbuga west of the lakes was urged by me and has been carried out, but a sufficient barrier has hardly as yet been made to account for the slowing of the advance. The absence of thickets referred to above may be the cause, in relation to a fly for which thicket commonly plays such a part in the vegetation-concurrence that it requires. Russell found here his dry-season concentrations, such as they were, in small areas of thicket country in association with water-holes; but it is by no means certain yet that, even if this were the case, advance cannot still proceed on

sections so far not examined sufficiently minutely, or that in a specially favourable season, the semi-unfavourable country may not become so infested as to form a bridge to the Rift Wall and the wooding below, including that about Lake Balangda Lalo.*

3.—AREAS SUITABLE AS A PERMANENT HABITAT FOR *G. SWYNNERTONI.*

Gordon-Russell formed the following theory regarding the nature of the areas suitable as a permanent habitat for *G. swynnertoni.* "As a result of the two surveys the opinion has been formed that only limited portions of the area are really suitable as a permanent habitat for *G. swynnertoni*, and that of these the largest is the so far uninfested area east of Lakes Basotu and Bassodesh and the Endamasak road. The area does not enjoy a heavy rainfall and dries up rapidly on the cessation of the long rains, causing a rapid defoliation of the bush. Strong winds blow almost continually throughout the long dry season from the east. These circumstances cause the fly to evacuate the country and retreat to the warmer, sheltered country below the Yaida depression escarpment and to the vicinity of the Endabash water-holes. Their evacuation is accelerated by grass fires. What cannot be understood is why they do not form concentrations around the shore of Lakes Basotu and Bassodesh, where conditions would appear to be ideal—permanent thicket shade and unlimited supplies of food. Fly were taken during the recent survey in the Dhangaid mbuga at a point only 2½ miles from Lake Basotu and within half a mile of the road. Fly were taken actually in the dense belt of gall-acacia and none in the *Acacia–Commiphora* wooding which joins the belt and runs to and beyond the lakes. Game and cattle in numbers graze in the Acacia country right up to the gall-acacia belt, the former of course actually in the belt and beyond. The fly taken certainly were without exception well fed and consisted of 99% males" (Gordon-Russell, report, 2.iv.32). The latest news available suggests that recently a heavier infestation has taken place on the west side of Lake Barotse.

4.—THE WORK DONE.

The work done consists of the surveys and clearings just referred to, by Gordon-Russell; and the inspection and advice given at different times by Potts, Burtt, Jackson, Vicars-Harris, and myself.

5.—RECOMMENDATIONS FOR FUTURE ACTION.

An exceedingly thorough re-survey of the entire position and all its details from the Singida border to Oldeani, the northernmost point of this great arm of the East Mwanza fly belt. This is definitely an urgent need. Findlay, it is proposed, might do the spade work, if Gordon-Russell has not the time, and an entomologist or I myself go over the ground with both afterwards with thoroughness. It is only such a survey as this that will really clear up the position. show its danger points and where it need not be attended to, and where and how the fly can be attacked. Such a survey will also undoubtedly add very greatly to our knowledge of the requirements of this fly and of how to deprive it of essentials. It will be of value both to the tribe and to the general problem. It will be recollected (*see* p. 433 above) that the southern end of this fly belt is advancing, very definitely, at Iambi on the north-eastern Singida border,

* This is marked "Balangida" on map 5. If the map covered a larger area, the new infestation by *G. morsitans* would be seen to be adjacent to it.

and, further, that with outbreaks existent already in the Mwanza portion of this belt and in Mkalama, the danger of sleeping sickness is not small. Gordon-Russell suggested that we should place one of our thicket barriers in front of this fly advance by demarcating a strip and keeping it unburned. I myself, while approving, prefer an attack on this entire belt by this means. But without a special officer resident on the spot with a very full fire-organisation there is no hope of holding up fires in face of the unruly Barabaig and the wild, under-sized Watindiga hunters of this area, even should it be possible then.

G.—THE ADVANCE BY *G. SWYNNERTONI* INTO SOUTHERN MASAILAND, NORTHERN PROVINCE.

Some years back the belt of *G. swynnertoni* which is shown in dark blue in map 1 south of the large-lettered word "NORTHERN," was known to be advancing in an easterly and south-easterly direction. Potts and Burtt carried out the necessary survey. The advance appeared to slow up following the deluge of May 1930, but, owing to lack of staff for reconnaissance, the present situation is uncertain. Nearly the whole of the vast light blue area shown on the map is believed to be liable to infestation by *G. swynnertoni*, though parts carry thicket enough to slow up an invasion.

This is the greatest threat in the Tanganyika Territory.

H.—GENERAL CONCLUSIONS AND VIEWS.

Approximately 2,000 square miles of country have been seized from the tribes of the Central Province by the tsetse in the course of the last seven years. The financial depression, which prevented money from being spent, has been partly responsible, though the too ready abandonment of the work undertaken in 1927 first allowed the flies to break through defences on which they could have been held.

The flies are still seizing country at, if anything, an accelerated rate, and I wish to state here my conviction, to be restated more fully under "Needs of the Work," that only by means of special experiments and some special expenditure shall we be able to evolve methods to deal adequately with these situations in future. At the same time, given money and the facilities for this experimentation, I am fairly sanguine of success.

PART 8.—CO-OPERATION WITH BRITISH AND FOREIGN TERRITORIES AND WITH AUTHORITIES IN THE TANGANYIKA TERRITORY.

A.—GENERAL.

The period mainly under report has been one of very free, if informal, co-operation with other territories. Our knowledge and our methods have so advanced that we are able to be of use to them. Conversely, conditions vary enormously and we draw at this stage great benefit from every variation of the problem of each of the species of tsetse that is seen by us and from the experience, discussed on the spot, of workers elsewhere.

Consequently the closest and friendliest co-operation has arisen between ourselves and Uganda in connection with *G. morsitans* and *G. palpalis*, and between ourselves and Kenya Colony as regards *G. palpalis* and *G. pallidipes*, the two chief Kenya flies, and has for five years continued.

As a result of visits, of continued correspondence and of a regular exchange of reports, typewritten and other, we have, for practical purposes and in so far as the medical and veterinary entomologists of the other colonies are able to devote time to tsetse work, almost reached the position of working loosely as separated members of a single team. It was suggested that, as regards this work, the inter-colonial boundaries should be disregarded. This suggestion has been agreed to officially.

Friendly exchange of information has taken place between Nyasaland, Southern Rhodesia and ourselves, and we have been able, I believe, to be of use to the Sudan, the Gold Coast and Fernando Po. Moggridge's visit to Italian Somaliland obtained the very friendly support of the Italian Government there, for which we are grateful, and visits which have taken place more recently are due again shortly to Southern Rhodesia, Nyasaland and Northern Rhodesia, in which latter colony we have been asked to investigate a problem.* In addition, through the publication of papers, we have disseminated the results of our work to all workers on tsetse, wherever they may be situated. Advice and co-operation are not confined to the so-called "cattle" tsetses, which are just as much "human" tsetses. They have been undertaken yet more prominently in the case of *G. palpalis*, purely "human," our measures against which fly have seemed particularly promising and a special co-operative experiment concerning which has been carried out in conjunction with the Medical Department of Kenya.

Between ourselves and the other organisations in Tanganyika concerned with trypanosomiasis—namely the Medical and Veterinary Departments—the very friendliest feeling exists. Co-operation in each case is both invited and given where it is needed and where staff permits. In this case also we serve both sides of the problem. Large consignments of pupae, needed by them, have been sent by us also to the workers on human trypanosomiasis in England, Germany, Uganda and Tanganyika.

In no case, whether as between ourselves and those working in other British territories or between ourselves and the members of the Medical and Veterinary Departments in Tanganyika, does appreciable overlapping take place. Not that some overlapping is bad: it is useful for confirmation and control.

* It has proved possible to include brief references to these visits in the present paper, on p. 325 (Nyasaland), p. 454 (Southern Rhodesia), and p. 509 (Northern Rhodesia).

The Tsetse Research Department has kept in close touch with people and bodies at home. Our plants go to Kew and the British Museum and in return we obtain identifications : the Imperial Institute of Entomology has identified parasites for us, we have been in correspondence with its Farnham Royal Laboratory in connection with parasite control, and we have remained in very close touch with the Institute generally. We have been in correspondence with Prof. Buxton of the London School of Tropical Medicine in connection with the effects of evaporation on insects, on which he also has been working, and Lloyd has attended a course with him. The Chemical Defence Research Department has regularly been consulted by us on one point or another and, in connection with our plant-poisoning experiments, we made touch with various chemists and physiologists, the School of Forestry in Oxford, the Imperial Institute, Professor J. B. Priestley, and the Prickly Pear workers in Queensland. Jackson, who took a course in statistics in England, has continued to keep in touch with Dr. Fisher of Rothamsted on the subject.

B.—THE JOINT EXPERIMENT BETWEEN KENYA AND TANGANYIKA ON MABOKO ISLAND.

1.—DESCRIPTION OF MABOKO ISLAND.

This has been given in full in the account of *G. palpalis* on pp. 129–138 above.

2.—PRELIMINARY INVESTIGATIONS AND THE SCHEME.

In May of 1932 a preliminary trapping experiment was carried out on Maboko Island in the Kavirondo Gulf near Kisumu, Kenya, by Mr. Symes and myself. Some of the results are given on p. 255 below. They were such that I recommended that the Medical Department, Kenya, represented by the Medical Entomologist, and the Tsetse Research Department, Tanganyika, should carry out a joint experiment in the control of *G. palpalis* on the island.

3.—THE WORK IN HAND.

A fly-round is carried out twice a week all round the island, the flies being sexed, "hunger-staged," marked and released; pupa rounds are carried out twice a week, the live pupae being marked and put back, and the traps are cleared daily. Very full records are kept.

4.—THE RESULTS SO FAR OBTAINED.

The work proper started on 20th October, 1932, when our fly boy, Milambo Kazila, Kwama of the Kenya Medical Department, and a third fly boy (ours) took up their residence and worked 16 traps. The work was more fully organised in November of 1932 by Jackson accompanied by Mr. G. L. R. Hancock (then Assistant Entomologist, Uganda) and in January 1933 when Messrs. Symes and Harper and I spent some time on the island. By November of 1933, *i.e.* one year after the first setting out of the traps, it was calculated from the fly rounds that the flies were already reduced by between half and two-thirds of their numbers by means of the traps. Progress since then has been slower and it is known that the broad, but arm-like promontory north of the island, which was left as a temporary control, has been much more popular with food animals and is providing steady re-infestation. Lloyd, by the recovery index, roughly estimated the population on the main island and on the promontory in October 1934. There were estimated to be approximately 6,000 males still on the former

and 3,000 on the arm. Pupa searches revealed more live pupae on the arm than on the main body of the island. " The arm has thus acted as a fly reservoir of the trapping area " (Lloyd).

This is another case in which money has been insufficient to complete the scheme of an experiment—in this case by means of an isolating barrier across the neck of the peninsula. In any case, it has not been visualised that the experiment could be completed without the presence on the island in the last few months of a European scientific officer, and no such officer has been available.

The results of the fly rounds and pupa rounds will be dealt with in a future publication. Meantime an extract from a report by Moggridge, dated 23rd June, 1934, may be quoted :—

" Practically all the traps are set on their sides as this (first tried by Milambo) has proved by far the best catching position. About five AS buttock traps are suspended and of these three, sited in favourable positions, are doing well.

" Comparatively small numbers of *G. palpalis* are now being caught in the traps, but this is thought to be due to the reduction in fly numbers rather than to ineffectiveness on the part of the traps.

" Milambo reports that whereas previously all the traps caught flies, at present the catching is confined to sections of the island, now here now there, as though, Milambo says, ' the tsetse had adopted the habits of locusts to fly about in swarms.' A very large proportion of the traps are therefore hardly catching at all.

" The reduction of fly numbers is indicated by the results of the pupa hunts. Whereas previously large numbers of pupae were unearthed now no more than five or six can be discovered at one time.

" Reference was noted in Milambo's reports and trap figures to ' Mitego ya pango.' The figures refer to the Chorley traps, which when laid on their sides have a cavernous appearance.* These traps are now not catching any flies at all.

" A fly round was done with Milambo and Hassani. Flies are still numerous on the island judging by the numbers captured. A considerable number of old females was captured.

" There is every indication that the high standard of efficiency and keenness that Milambo has hitherto shown is being maintained."

From a later report of Lloyd's :—Milambo stated that " in the early months of the experiment when the flies were very numerous it was quite impossible to catch all the flies that came to one." This is a vitiating factor as regards the reliability of the rounds as an index of density at the start and density now. The reduction has probably been much greater than our recording shows.

Catches by traps. Heavy catches were made by the few traps put out temporarily in May. The 16 traps of October 1932 were increased to 20 in November, 30 in December and, gradually, to 60 in January. They remained at this figure till May 29th of 1934, when 40 new traps were added. 100 traps may be regarded now as the average potentially effective total.

5.—COMMENTS ON THE TRAP RESULTS.

The higher figures from February to July (1933) and to September (1934) are being repeated in 1935, the rise now coming in March. These, and the low periods between, correspond well with the high and low periods on Riamugasire

* *See* pl. 8, fig. 5.

TABLE 66.

Monthly catches of *G. palpalis* in traps on Maboko Island.

Month	Males	Females	Total	Female %	Average per day	Average per day per trap
1932.						
October	974	354	1,328	25	111	7·0
November	1,372	650	2,022	32	64	3·2
December	3,095	1,788	4,883	37	168	5·6
1933.						
January	9,101	6,384	15,485	41	484	10·68
February	12,702	13,458	26,160	52	902	15·00
March	11,358	11,647	23,005	51	742	12·50
April	3,410	3,188	6,598	48	225	3·75
May	2,248	2,426	4,674	52	146	2·43
June	1,603	1,357	2,960	46	109	1·82
July	1,380	1,083	2,463	44	77	1·28
August	699	449	1,148	39	37	0·62
September	588	430	1,018	42	32	0·53
October	304	225	529	43	17	0·28
November	628	337	965	35	27	0·45
December	473	337	810	42	25	0·42
1934.						
January	855	549	1,404	39	43	0·72
February	1,062	804	1,866	43	67	1·12
March	2,021	1,985	4,006	50	125	2·08
April	2,877	3,372	6,249	54	223	3·72
May	2,661	3,652	6,313	58	204	3·40
June	2,785	3,285	6,070	60	190	2·38
July	1,678	2,332	4,010	58	129	1·29
August	1,895	2,724	4,619	59	165	1·65
September	1,474	1,886	3,360	57	105	1·05
October	746	889	1,635	54	59	0·59
November	772	778	1,550	50	48	0·48
December	515	467	982	48	32	0·32

Island. The low totals in October 1932 were due to few traps. The drop in numbers in the "high" months in 1934 as compared with the numbers in the same period of 1933 is certainly a trapping-out effect, which, however, has not been accentuated adequately in 1935. The column giving the catch per trap cannot be regarded as giving more than a rough result, as new batches of traps each took some days to erect through shortage of staff, crocodiles broke many traps that were set on their sides, it was not always possible to re-upholster bleached traps at once in the gaps between the visits of officers, and much repair was found to be necessary when our carpenters from Shinyanga finally went over the traps in February–March 1935. Ants and lizards were a differential trouble as well, especially when the traps were set on their sides, dragonflies probably took great and varying toll of the flies on the screens, and in any case it constantly happened that a single trap was responsible temporarily for nearly all the captures on a section, catching really high numbers while the others caught practically nothing, and indicating that these others were for the time being superfluous. This, chiefly, accounts for the very low average catch. While the natives did splendidly, had it been possible to have a really good

European naturalist observer in charge, a prolonged study of the causes of these differences and a continual judicious shifting of the traps would probably have brought the work to a successful close some time ago.

As regards the damage by crocodiles a recent experiment by Lloyd in raising the traps, still in a recumbent attitude, to allow these animals to pass underneath, was successful, the catch not being affected.

6.—THE DISTRIBUTION OF THE WORK AND ITS FINANCING.

Broadly the position has been this. We have supplied the head fly boy, Milambo Kazila, and a second fly boy, also the traps. Kenya has supplied a third fly boy and the Senior Medical Officer, Kisumu, keeps a benevolent eye on and devotes a helping hand to, the natives. We pay for the sailing-boat, which serves as liaison with the shore, building and repair of camps and all other incidental expenses. Visits are paid at intervals by Mr. Symes or one of ourselves.

7.—FUTURE PLANS.

It is intended, when a European is available for residence on the island, to use discriminative clearing, at first in the patches of more massive lake-shore thicket on the peninsula, and gradually to work down to finally exterminative measures. Probably (as was anticipated from the start) hand-catching off screens will be necessary to get rid of the last flies in the part of the island that is being trapped, when the traps have done all they can under the system of observation and shifting suggested above.

C.—SOME OF THE SITUATIONS ADVISED ON, OR SEEN IN, KENYA COLONY, UGANDA, SOUTHERN RHODESIA, AND ZULULAND.*

1.—THE KUJA RIVER SCHEME IN SOUTH-WEST KENYA FOR *G. PALPALIS*.

(a) Description of the locality.

The Mirogi flows into the Pala from the north-east, and the Pala and Nthiwa, after running in parallel courses south-eastward, join and turn south-west into the main river, the Kuja.† The width of fringing thicket increases from narrow to very broad in the order in which these streams have been mentioned. It is very wide on the Nthiwa and Pala after they join and on the Kuja. The types of vegetation that fringe these streams and occur in the country between have been roughly described on pp. 155–157 under the heading of *G. palpalis*. The fringing thicket generally was infested with this species of tsetse.

(b) The history of the scheme.

Mr. C. B. Symes, Medical Entomologist, Nairobi, conceived a scheme for the clearing of the fords and, if possible, the expulsion of *G. palpalis* from the Nthiwa and other tributaries mentioned and from the Kuja itself. I myself was called in to advise, and did so in May 1932.

During my week on the Kuja with Mr. Symes, traps of nine types of our own were tried against each other and against the Harris trap at the Oredi ford of the Kuja, and my SS (or AS) trap (pl. 2, fig. 3) was selected as

* Fair detail is given in most cases, such as for the reclamation projects in Tanganyika, with a view to placing on record the position existing at the present time. For others interested in tsetse control, the combinations of measures that to-day are being tried or prescribed in relation to different sets of conditions will be of value.

† This is shown on the upper portion of map 1.

being much the most successful. The scheme eventually worked out is described below.

(c) Recommendations submitted.

"(i) The fords should be cleared, as had been intended, to avoid contact with 'fly' by the natives using them. The ford clearings, if wide enough, would act also as barriers and the dense strip of riverine thicket that in varying width followed the rivers and harboured *palpalis* would thus become split into blocks.

"(ii) Definite experiments should be tried in varying the widths of the clearings from say 500 yards to 1,200 and if necessary more, marking large numbers of flies and then seeing, by means of catches and traps, if they cross from one side to the other."

"(iii) In the blocks into which the clearings of the fords would break the riverine thicket intensive trapping should be carried out against the flies. "Adequate clearing of the fords will leave narrow river-reaches isolated. . . . Taking one of these at a time, I am convinced that (if adequately isolated) it will be possible to clear it of *G. palpalis*. This species enters suitable traps . . . readily . . . its riparian flight makes it easy to intercept it, and the fact that it follows paths should enable it, through the making of these judiciously, to be concentrated on to very few traps. . . . The flies that may continue to elude them can be finished by native catchers [with screens] in a much reduced period and, therefore, at a much reduced cost and, the flies being scarce, with a greatly reduced risk of infection. . . .

"(iv) A fly round, with boys, should be instituted through each of these strips to obtain touch with fly density at the outset and keep touch therewith afterwards.

"Given success in this experiment, the process of clearing out the fly could be applied to strip after strip between fords, first down the tributaries, later down the Kuja to the lake and along the lake-shore if desired.

"Difficulties inadequately foreseen at this moment will certainly be met with, but the problem of each strip is so small compared with that of the blocks of country we are dealing with in Shinyanga against a more difficult fly that I cannot believe that success will not be attained."

(d) The work done.

Mr. R. T. Vane, previously of our Department, was recommended for the supervision of the work and proceeded to the Kuja in October 1933. He has since remained there in charge under Mr. Symes.

Seven fords have been cleared. The first attack on a strip between clearings was made on Block 2, not Block 1, and by hand-catching as the traps were not ready. Weekly fly rounds were carried out. Great numbers of flies have been marked.

(e) The results so far obtained.

(1) Great difficulty is experienced in maintaining new clearings in a year of good rainfall, rank climbers that quickly cover the felled trees being the trouble in the clearings generally rather than woody regeneration; also quick up-growth of reeds and rank herbage on the stream courses.

(2) Great numbers of flies have been marked and the passage of a small percentage of flies across clearings and between the Nthiwa and Pala tributaries has been demonstrated. Widths were crossed of at any rate 850 yards. The coming down of the river in flood caused special activity each time and an increased catch of marked flies on the wrong side of a clearing.

(3) Generally speaking, hand-catching is far more efficacious than trapping, especially when, as in Block 1 initially, and in other blocks later, the numbers are low. In Block 2, in which 1,522 flies were caught in October of 1933, the flies have become so reduced that in the last four months recorded only 16 were caught.

(4) As we have found elsewhere, there is immense variation in the catches of exactly similar traps placed in different positions, with nothing, so far, to account fully for the differences.

(5) Despite difficulties " the Nthiwa, Pala and Mirogi Rivers (especially Block 2) above Wadhasaa clearing have been practically cleared of fly " (*see* p. 508).

(f) Finance.

This scheme and the following (Lambwe valley) scheme, with clearings in middle Kavirondo, are being financed from a sum of £6,000 granted to the Kenya Government from the Colonial Development Fund for the purpose.

2.—THE LAMBWE VALLEY SCHEME IN SOUTH-WEST KENYA FOR *G. PALLIDIPES*.

(a) Description of the locality.

The Lambwe flows from a point not far north of Karungu, a small port on the east shore of Lake Victoria, into the Kavirondo Gulf close to Mount Homa. The following is taken, with slight condensation, from a report written by me after my visit thereto in October 1932.

The valley, running between two lines of high hills that are fairly devoid of bush above and should form quite good barriers, appears to be about sixteen miles long. Along the seasonal stream which flows down the centre is a thicket, in parts wide, in parts narrow. Often thickets, small or extensive, occur on each side of this and between is very open savanna bush of *Acacia* (including *seyal*).

On the sides of the hills are some wooded ravines, some thicketed outcrops of rock and (on the fan slopes at their feet) some areas of scrub. The flies (*G. pallidipes*) are probably using these in small numbers as well as the valley wooding and thicket which doubtless form their real home.

Just down the valley from Suro, still in Gwasi, the riverine thicket is very narrow—perhaps three-quarters of a mile.

(b) The history of the infestation.

The Chief of Gwasi, Kasuku, told me that up to about 60 years ago the valley was so heavily populated that the bush was kept down. Cattle were kept throughout it. At that time his people (who had come from Uganda) embarked on a series of attacks on the other inhabitants of the valley and drove them out. There followed the usual nemesis, to be seen equally to-day in Tanganyika in the districts of Shinyanga, Nzega and Southern Masailand whence population has been expelled. The bush grew up and the fly, somewhere surviving, came in and infested the valley. It appears to have only advanced into the head of the valley recently. The Chief attributes this advance to the elephants and buffalo, but *G. pallidipes* is a very free rover and, while the elephants, in the numbers in which they were lately present, will have assisted much, it would, with any food present, have come up without being carried. The elephants in the local herd, which was recently driven away by Dawson, were reliably estimated to have numbered from 800 to 1,000 head.

Whatever the cause of the movement of the people, it is said to have involved the departure of the inhabitants of 360 villages from Gwasi alone.

(c) The work done previously and comments thereon.

The following work had previously been done. The Gwasi people had made a clearing, about 700 yards by 700 or rather more, in very dense bush away from the river in the valley opposite Suro. It was proposed to carry this clearing, greatly widened, across the valley. At the moment the workers are *re*-clearing what they have done, as it has grown with the utmost rapidity into dense scrub behind them.

The following comments suggest themselves. (α) It is obvious that there is not the man-power here to carry out extensive clearings all over the valley. Other means must be used, in the main, to get the flies out. (β) It is obvious also that it is useless clearing this thicket unless you can settle it closely and permanently. There is not enough top hamper to make a sufficient fire round every shrub-stump to kill it, and poison in this type of close thicket is too expensive (*see* p. 412).

(d) The scheme and the recommendations.

(i) *The general scheme.*

Break off a piece of the bush of manageable size at the head of the valley by means of an adequate permanent clearing and try and clear it of fly.

If this succeeds, extend the process to a further section and then to a further; but the first piece, being the most experimental, will take a few years and should be concentrated on very completely.

The narrowed thicket strip referred to above is the obvious site for the clearing. The latter should be made wide enough.

(ii) *The details of the scheme.*

The details of the scheme are as follows :—

(α) Map the bush areas that would be included in the clearing just referred to, the dense thicket and the types of savanna separately, right across from hill-top to hill-top. Look out for *G. pallidipes* in the hill-side pieces and for *G. brevipalpis* throughout.

(β) Decide, on this survey, whether enough man-power will be available to cultivate with low crops the dense thicket sections of the proposed clearing.

If it is available, definitely, the settlement scheme should be planned in detail right away. If it is not available it is useless to clear the thickets.

(γ) Stop all other clearing in the valley and concentrate all labour on the Gwasi barrier clearing.

(δ) Without fail provide unbroken European supervision for the clearing and the subsequent measures. Long experience shows that without adequate white supervision the work is badly and impermanently done and with great waste of labour.

(ε) From the start, plan for, and insist on, permanent methods of cultivation. Shifting cultivation would, later here, wreck the whole scheme. In other words bring in the Department of Agriculture from the start.

(η) Place traps in the break-through clearing, when it is complete, to test its efficacy.

(θ) Carry out very thorough entomological surveys of the bush-area to be separated from the rest of the valley by this barrier, before and after the barrier is made, and during the progress of subsequent measures.

(ι) Watch our work in Shinyanga and try the same methods—*mutatis mutandis*. In the meantime try out fly traps and screens.

(κ) As regards the game, I recommend leaving it alone for the moment, except for such shooting as may be necessary to protect cultivation. It is important, in order to get a proper appreciation of the measures that will (we hope) have exterminated the fly, that the entomologist in charge should be provided with natural conditions. He will himself recommend the destruction or driving away of one or more species of game should he later find it to be necessary, and valuable lessons, for application elsewhere, will meantime not have been lost.

(λ) If tribal labour is used, it is very important (we have found) that it should not be discouraged by being kept out too long, or at sowing or harvesting periods, or put on to jobs which will not be carried through to success. Tribal labour in Tanganyika is proving most useful, but the numbers available are great, and even there paid labour is a good deal more efficient. The Gwasi people are few, and this raises the question whether money may not be available to hire labour instead.

From earlier recommendations : " that the whole bush west of this clearing should be the site of a thoroughgoing investigation of fly density, movements, habits, food- and vegetation-relations, lasting a year and aided by traps; secondly of an equally thoroughgoing attempt [afterwards] to exterminate the flies contained in it, by traps, catching at screens and other means that may commend themselves."

(e) The present position.

Mr. Lewis carried out the first entomological survey, and Commander Blunt, transferred from our Department, was, under Lewis, given charge of the work in January 1935.

3.—THE KENYA COASTAL STRIP.

(a) The preliminary investigation.

A visit was paid to Kwale, the Shimba hills and Kinango in the cattle country to the west of these in September 1932 with Dr. Phillip, Messrs. C. B. Symes, E. A. Lewis and Mr. Hassan. A quite good general idea was obtained of the situation from coast to cattle-belt, but without time for the examination of detail.

On September 29th, accompanied by Mr. Symes and Mr. Lewis, I went up the coast road to a point a few miles north of Kilifi, to gain some impression of the problem in that direction.

I am indebted to the officers mentioned and to Mr. P. B. Foster, Assistant District Commissioner, Kwale, and Mr. McNaughten, Assistant Conservator of Forests, for much help, information and hospitality.

(b) Description of the general problem.

The problem of the coast and its history is as follows :—Formerly the strip between the coast and the coast hills was, it seems, fairly generally free of fly as the result of the intensive cultivation by means of slave labour under which it was placed by the Arabs. With the abolition of slavery a great deal of land has relapsed to savanna bush and dense thicket, and the greater part of the area * is now infested with *G. pallidipes*. *G. brevipalpis* and *G. austeni* are generally present as well.

* This is marked as " coastal debris " on map 1.

For dealing with the coastal tsetse problem northward to Ganzi, it is of great importance to be able to split the country into strips or blocks of more manageable proportions than the whole fly area. It would be much more difficult to deal with the coastal fly belt were there no fly barrier between it and the main belt further west and no potential barriers across it. Fortunately such barriers exist. These are :—

(α) The sea on the east, with, from Mombasa southward, a strip of rather unsafe cattle country flanking it.

(β) A strip of easily-cleared country some miles long along the top of the Shimba hills, more or less parallel with the sea front and perhaps capable of splitting this part of the coast tsetse belt longitudinally.

(γ) A long and broad strip of cattle country extending from near the Tanganyika border at Mwena to a point (Ganzi) north-west of Kilifi and separating the coast belt of tsetse from the far broader main area which runs back past Voi.

(δ) Interspersed in the coast belt great areas of present and past cultivation, rendering it easy with a minimum of extra development or special clearing to make barriers across the belt and so split it into blocks, or to clear up the belt nearly completely.

In addition fair to good soil and good rainfall are present throughout, with access to water transport, rendering development easy.

(c) Recommendations.

(1) A very thoroughgoing agricultural survey of the Coast strip from the Tanganyika border to Sokoke, if this has not already been carried out. A tsetse-fly survey and experimentation in trapping the flies.

(2) A real push with the organised agricultural development of the strip from Sokoke to the Tanganyika border. In native reserves the natives would be encouraged to push forward with the cultivation of the appropriate economic crops. To areas owned by European companies measures would be applied to discourage the continuance of the disuse of the land. In other areas whatever steps might usefully be taken to promote development would be taken. Adequate Agricultural Officers to ensure thorough and appropriate development should be supplied if the scheme comes into operation.

(3) When the development has reached its maximum, islands of fly will remain, *e.g.* in the form of forest reserve, steep scarps and ground that for other reasons cannot be developed. These "islands" would then be subjected to entomological work.

(4) A clearing of the easily-cleared hill-top strip running past Kwale into the Golini Reserve if it has not then already been done. The head of the Mombasa water-supply would be excepted from this.

(5) That the Forest Department should be approached with a view to a postponement of their planting programme at Kwale pending entomological survey, and to its possible ultimate cancellation. (As planned it would create a connection between fly belts across one of the strips just referred to.)

(6) The fly belt west of the Mwena–Ganzi barrier; and the Tana river. The first of these areas is enormous and is, for the most part, I believe, country the development of which will not be demanded for a very long time. It would be best, therefore, to leave it completely—as regards any general measures—till experience is gained.

(7) The Tana river. Surveys were actually being made at the time of my visit with a view to the development of this valley.

(d) Survey.

I judge from the maps I have seen that there are many gaps yet to be filled in the knowledge of the distribution of tsetse in Kenya. Survey with a view to filling them should, I suggest, be quietly pushed on with against the day when money may be available for extermination where this is needed. Possible invasions of new country should in particular be watched for.

(e) Research.

It has been arranged, with the kind permission of the Kenya Government and Veterinary Department, that we should station Moggridge at Kilifi and that he should carry out there our own investigation of the habits of *G. pallidipes* and (incidentally) of *G. austeni* and *G. brevipalpis*.

4.—KWALE, ON THE SHIMBA HILLS, AT THE BACK OF MOMBASA.

(a) Preliminary inspection.

I visited this place also, by request, in October of 1932. Kwale, including its tribal settlements, was the subject of some very advanced and very successful experiments by Dr. Phillip in malaria control, and he, and the Veterinary Department, were anxious to take action about the tsetse. Moggridge, who has stayed there since, has described the natural situation as follows :—

(b) Physiographical features and vegetation.

The Shimba hills, some 18 miles west of Mombasa, form a high tableland about 4 miles broad and perhaps 15 miles long. The slopes of the hills are in many places very precipitous and give rise to steeply sloping valleys. The top of the plateau is flat, and scattered about this area are many patches of rain forest of various sizes. In some cases the forests are confined to the plateau, but in others they extend down the hill slopes. The narrow valleys are lined with dense lower thicket, and clumps of thicket of various sizes are scattered at random about the area. Open grass-land obtains in the absence of thicket, more particularly on the higher ground, but often also the thickets are connected up by light patches of savanna of *Bauhinia*, *Vitex*, *Strychnos*, *Ormocarpum*, *Anona*, *Albizzia*, *Dalbergia*, *Dichrostachys*, *Fagara*, *Randia* and *Thespesia*. I do not know what were the species comprising the rain forests, although *Chlorophora excelsa* (Mvule) and *Sterculia appendiculata* (Mgude) were noted. The composition of one forest, that of Kipunguni, differed greatly from that of the others and seemed to be composed of a high percentage of *Berlinia* sp.

(c) The fly situation.

The forest patches, thickets and other wooding are infested with *G. pallidipes* seasonally or permanently in large numbers or small.

At the time of Moggridge's visit (26th Nov. to 8th Dec., 1934) careful and continuous reconnaissance failed to produce other than a very occasional fly from the valley thickets and thicket clumps, and comparing the number of *G. pallidipes* caught—in all three—with the area of this type of thicket covered, one would be justified in asserting that tsetse are absent therefrom at this season of the year. Tsetse were encountered only in the main rain forest. Density in the forest of Shimba and Ndawa which adjoins it proved to be extremely light. . . . A catch along the side of the forest of Makadara . . .

produced no fly. . . . The forest of Longo Mgandi provided the only centre where fly were encountered in any density . . . 14 *G. pallidipes* per hour.

It is doubtful whether in this case the apparent density gives an accurate reflection of the actual density of *pallidipes* present in the forest, for the reason that the flies were almost all replete and the majority appeared to come to the party more out of curiosity than hunger. A large number of flies were caught off the ground and off grass blades only after prolonged "spooring" by the sound made in their short flights round about the party.

At the time of my visit, in October, flies were judged to be more plentiful than Moggridge found them to be. Moggridge surmised "that all the riverine thickets and thicket clumps may be fly-infested at the end of the rains and that the forests themselves would then show a great increase in density." However, "the flies taken in Kwale area [by Moggridge] were all surprisingly replete." *G. pallidipes* in a state of repletion comes rarely to man, so that even the density in November was doubtless much higher than appeared.

(d) The problem on which advice was requested.

It was hoped that it might be made possible for the Administrative station of Kwale and the tribal settlements of Golini, close by, to keep cattle. It had been suggested previously that the cattle might be kept in by day and grazed out at night in the open grassy spaces between thickets in a stretch of country between the station and the native settlements.

(e) Recommendations submitted.

I took the view that the proposal to graze the animals at night was subject to the following disadvantages:—

(1) *G. pallidipes* apparently feeds on moonlight nights. I have experienced attacks. This would mean that for a large part of each month the cattle could not be let out at night.

(2) On dark nights the herd-boys could not be trusted to keep the animals away from the forest edge and from clumps of bush which may contain fly. The latter might attack even on a dark night if disturbed.

(3) *G. pallidipes* comes to conspicuous objects and is probably attracted by scent.* That is, it may visit the cattle in their shed in the daytime if the latter is not surrounded by a clearing. Its openings could, of course, be wire-gauzed and the cattle not be let out at all.

The clearing of a strip beside the Golini Native Reserve was suggested. It was subject to the disadvantage that from the Golini villages to the thicket scarp to the east is not a very wide strip, and that the coconuts, mangoes, etc., at the villages form conspicuous masses that might attract the flies. Open coconut plantations covering a great piece of country are not so dangerous. Close up to the natural fly bush dense plantings such as these may be dangerous.

The clearing to be part of a larger clearing extending south to the station of Kwale. This latter part of the clearing should be made and tested first, and the water should be cleared to 400 yards at least *on each side* of the drinking-place and at least to this distance back. The cattle shed or kraal would be in the centre of the main clearing, preferably in an inconspicuous place, as a hollow.

Very little clearing, comparatively, is needed in this park-like country.

* *See* pp. 204–206.

The clearing was to be regarded as experimental, as *G. pallidipes* was expected to cross wider clearings than *G. morsitans* or *G. swynnertoni.* However, the results obtained since in Melsetter in Southern Rhodesia and in Mpapwa rather belie this expectation and make the clearing suggested for Kwale more hopeful.

(f) The present position.

I have not heard of the action, if any, that has been taken, but if Moggridge, who will be stationed at Kilifi, and will have to visit Kwale in connection with his general study, can assist in clarifying the situation further, I shall be glad to offer his services.

5.--LANGO, UGANDA.

(a) Jackson's reconnaissance.

A recession of the flies had some time previously taken place here.

" This visit was made in October–November 1932 at the invitation of the Veterinary Department of Uganda. Generally modifications were suggested in details of reclamation schemes projected and in progress, and the technique of ' fly ' surveys and kindred matters was demonstrated to the officers in charge of the operations. Meanwhile, two interesting areas infested by *G. morsitans* were seen, different in character from any in Tanganyika, as well as some country from which this species had been receding for some years. Unfortunately it was not possible in so short a time to suggest any reasons for this recession in Lango."

(b) The vegetation.

" In Lango, in a bend of the Nile where that river emerges from Lake Kioga in northern Uganda, *G. morsitans*, with *G. pallidipes*, was found established and breeding in low hills covered with *Combretum* spp., massive thickets of *Rhus*, *Grewia*, *Harrisonia abyssinica*, *Rhamnus*, and *Gymnosporia*, and very long grass. In more open places, under *Acacia campylacantha*, *A. hebecladoides* and *A. seyal*, feeding-grounds were found. The belt seen was actually one of two which have become separated in recent years, leaving between them an ever-widening gap of uninfested country."

(c) The fauna.

" Jackson's hartebeest and oribi predominated. Other animals included black rhinoceros, a few giraffe, and some bush-buck and wart-hog. Lack of game did not account for the recession."

(d) The tsetse position.

" Unfortunately, the weather was too wet for many hungry flies to be found, and it was consequently difficult to make out the anatomy of the fly belt, while long grass and the absence of bait-cattle prevented any thorough investigation of *G. pallidipes*."

(e) Recommendations submitted, and work at present being undertaken, by the Veterinary Department.

" A survey with bait-cattle was advised after the grass fires in February. Meanwhile it was suggested provisionally that certain clearings might usefully be made with the object of cutting off from the main seat of infestation certain large outlying areas then frequented by wandering flies probably incapable

of permanent existence in them, but sufficiently numerous to prevent the keeping of cattle " (Jackson).

" The control of indiscriminate grass burning in Maruzi, Lango, shows progress and the firing of 1934 was reasonably thorough " (Poulton).

6.—SOUTH ANKOLE, SOUTHERN UGANDA.

(a) The fly belts attacked by the Veterinary Department.

South Ankole was characterised by several small belts of *G. morsitans* that lay confined between high nearly bare grass hill ranges. These, working east from the Belgian Ruanda border to Nsongezi and thence north to Mbarara, were as follows :—

(1) *Kakitumba*, at the entry of the Kabobo river into the Kagera at the point at which the latter emerges from contact with Belgian Ruanda and the road to the latter leaves the main road.

(2) *The Ntundu valley*, forming the embouchure of the Kabigando valley (river Kivimbiri) into the open plain that here lines the Kagera, between Robarogota and Kikigati on the road.

(3) *The Ebitatenge valley*, which runs from near Lake Nakivali on the north to the Kagera at Nsongezi, at the point where the Mbarara road, running south, strikes that along the Kagera.

(4) *The Lugeye-Masha belt*, immediately south-east of Mbarara.

(b) The vegetation.

The general vegetation in these belts was *Acacia hebecladoides* savanna. From these trees, in the fourth-named belt at any rate, hung festoons of Old-man's Beard Lichen (*Usnea*), indicating a moderately moist climate. Scattered through the savanna were numerous clumps of thicket based on ant heaps and consisting predominantly of *Rhus glaucescens*, *Carissa edulis*, *Grewia* spp. and *Dombeya* with climbing *Jasminum*, *Cissus*, and *Senecio*. Candelabra Euphorbias of the *bilocularis* or *ingens* group are in parts very common in these thickets. Some of the rivers, as the Lugeye, carry more continuous thicket.

(c) The object of the attack.

The object of the attack was in each case the protection of grazing endangered by the flies, or the acquisition of grazing.

(d) The scheme of attack.

The system adopted in most cases, following thorough survey by R. J. Simmons and J. T. Kennedy respectively, was to clear the areas of greatest fly density which were regarded as permanent foci and the main breeding-places also. In some cases, as that of the Ntundu valley and Kakitumba, the clearings involved a considerable proportion of the area locally infested. In one area, that of the Ebitatenge, the clearing took the form of a barrier to cut off what was believed to be impermanent incursion of the flies from the Bigasha further east. The fourth problem mentioned in (a) above was the most interesting, partly on account of its greater size, partly because a lesser proportion of the wooding was cleared than in two other cases, partly because the dense wooding on the Lugeye was regarded as a barrier to the flies and extended further by means of clearings. Amongst other clearings made in this belt, the narrow valley of the Lugeye between Lwemikaka and the Mazinga swamp, with its mbuga feeding-ground

running down its centre, its " home " on the lower hill-slopes on each side, its open-margined swamp at one end and its own special herd of buffalo, struck me as the most complete *morsitans* fly belt in miniature that I had seen.

Organised grass burning of the whole belt on the Shinyanga lines was to follow the clearings.

(e) The first results obtained.

In every case amelioration of the position immediately followed the attack. The flies were reduced and the areas infested suffered contraction. In the Lugeye–Masha belt the creation of the clearings was followed by a tendency on the part of the topi and oribi to use them and so place themselves largely out of reach of the flies.

(f) Game observations.

" The passage of rinderpest through the susceptible game of the area had no effect on *G. morsitans*, and catches during and after the passage of the disease remained on the same lines as before till other factors intruded." The buffalo were hard hit and the wart-hogs, " very numerous before the coming of the rinderpest, lost heavily."

" An observation made as to the species of game animals frequenting the sections in which *G. morsitans* were more numerous inclined to influence the observer towards a hypothesis that all species of game are not equally bound up with the life of *G. morsitans*, and that their degree of usefulness to this fly depends largely on their habits " (extract from an unsigned copy of a report). The localised species with regular habits are the most important to the tsetse. " The hypothesis is that the buffalo, the bush-buck and the wart-hog are the species on which *G. morsitans* is mainly dependent in this area." Eland (migratory and irregular in habits), water-buck, topi and oribi, possibly zebra, largely out of reach of the fly, at least when provided with clearings, were here probably much less important.

(g) Further work and later position.

Fly rounds, a fly post, a continuance of the policy of controlled late burning, the settlement of natives in the clearings, some killing of wart-hogs and buffalo and (in connection with cultivation) the baboons, and the protection of the antelopes in the areas provided with clearings were amongst the decisions for the future. It is, in short, an experiment in discriminative clearing on very broad lines combined with some discriminative game-killing and with late organised grass burning. The position according to the latest reports was that the successive late fires were opening up the fly cover greatly even in the uncut bush, that, except for a very few stragglers, the flies had disappeared in the clearings, and that elsewhere generally their numbers were continuing to decrease (Poulton).

Organised grass burning shows very great promise in Uganda.

Several members of our team have been taken over this fine piece of work at different times by the Director of Veterinary Services, Mr. W. F. Poulton, or by Mr. Simmons or Mr. Kennedy. We have offered suggestions and been grateful for the experience.

(h) Finance.

The operations were financed by a grant from the Colonial Development Fund.

7.—THE POSITION AS SEEN IN SOUTHERN RHODESIA.

I was very kindly taken over parts of the ground by Mr. R. W. Jack, Chief Entomologist, Southern Rhodesia, early in 1923 and again in May 1931. On the first occasion the Darwin District was visited, on the second Gatooma.* The flies, from the limited areas into which their distribution had contracted at the time of the Great Rinderpest of the 'nineties, had steadily been re-invading the northern third of the Territory—all of which they had occupied previously. The threat was exceedingly serious both to established European settlement and to native reserves. On Mr. Jack's recommendation two game fences, ten miles apart, had been created in advance of the fly front and the game in between was being destroyed by European rangers assisted by trained native shooters. A ten-mile width was found to be not enough everywhere to prevent the spontaneous passage of a proportion of the flies, even with the game reduced to the lowest numbers possible, and the space was increased to twenty miles. This, as recorded elsewhere (p. 226), has been successful, but entails continual vigilance and expenditure. It was needed as an emergency measure, and it is difficult to suggest what else could then have been done, seeing that (*e.g.*) densification into thicket was, in most of the country shown to me, unpromising, and that organised grass burning had not been found a success. It has struck me, however, that an intensive investigation of the relations of the flies to the country, such as Jackson is carrying out in South Tabora and has been described on pp. 77 and 78 above, might have suggested a solution on the lines of discriminative clearing, which, initially more expensive than the annual Rhodesian expenditure, might have produced a more permanent result. Only such investigation can show whether such a solution is possible.

It may be said, as an addendum, following a visit in 1935, that I then found that it was proposed to push the fly over the Zambesi scarp and then cease to move forward. I suggested that if large forestry schemes should be afoot for Southern Rhodesia it might be considered whether plantings of densely-growing conifers, or their equivalent in relation to the tsetse, might not then be planted above the escarpment to cover the points or stretches up which entomological investigation might show that the flies tended to ascend. The broken nature of the country and the dryness of its climate are difficulties here in the way of this suggestion. It is nevertheless a useful one for areas to which it applies, and it should, in all such cases, be considered.

8.—THE POSITION AS SEEN IN ZULULAND.

I am much indebted to Mr. R. H. T. P. Harris and the Natal Provincial authorities for having allowed me to see the position existing in Zululand on two occasions—early 1923 and March 1931.

The Umfolozi area, which alone was visited, contains a small triangular game reserve between confluent rivers that is bounded immediately by a buffer area ten or fifteen miles across and, outside this, is hemmed in by blocks of European farms and by native reserves. The game reserve and its buffer contained very great quantities of game animals and *G. pallidipes* in very high density. The surrounding settled areas kept losing cattle heavily and, on very full search, odd tsetses were found here and there. There was a sparse infestation for which the wandering of game animals into the settlements was blamed.

Actually there was a great tendency for the game to wander outwards in time of drought from their reserve, for the latter, at such times at any rate, was

* And since this was written, Lomagundi and Gatooma again—in August 1935.

very much overstocked. Reduction was necessary and a great reduction was carried out.

Also, however, we have ourselves inferred from observation that the greater the density of tsetse flies the more formidable is the number of those that wander forth from the main body, whether spontaneously or assisted by game, but, we believe, mainly the former. It will be seen, therefore, that we have here, in Zululand, one of the few instances in which a mere heavy reduction of the flies, as opposed to their complete extermination, will be of use; for with the flies reduced to very small numbers the diminutive total that will still wander out will be capable only of negligible damage.

We have done enough work in Tanganyika with traps to feel that these, under our conditions, will never exterminate the tsetse. On the other hand, they are doubtless capable of converting a dense population of either *G. pallidipes* or *G. palpalis* into a small one. It is therefore probable that the Zululand reserves constitute one of the few cases in which traps can be expected really to mend a situation. The Harris trap is particularly excellent for *G. pallidipes*, and it is pleasing to learn that the campaign with it there which was interrupted by necessary economy is likely to be resumed in real earnest.

9.—THE KRUGER NATIONAL PARK.

A visit to this splendid park—a model for our future parks in east Africa—and the possible bearing of brief observations made there on the tsetse problem is described on pp. 219 and 220 above.

D.—CONFERENCES ATTENDED.

1.—CONFERENCE REGARDING *G. PALPALIS* ON MABOKO ISLAND, 18TH–19TH JANUARY, 1933.

Those present were Messrs. C. B. Symes, Medical Entomologist, Kenya Colony, G. L. R. Hancock, Assistant Entomologist, Department of Agriculture, Uganda, C. W. Chorley, Sleeping Sickness Inspector, Uganda, J. O. Harper, Field Assistant to the Medical Entomologist, Kenya Colony, and myself. The discussions were informal and the proceedings included visits to and participation in the work in progress on the island.

It was agreed to suggest that the Tsetse Research Team, Tanganyika, could best undertake parasite work combined with a general study of *G. palpalis* at Musoma; continued study of trapping; continued participation in the experiments on Maboko Island; and assistance, by suggestion and guidance, to the entomological side of the tsetse work in Uganda and Kenya.

Kenya Colony's share would be the clearing of fords on the Kuja river and its tributaries and of landing-places in Central Kavirondo, and the prosecution on the Kuja of the trapping-out experiments between clearings; continued partnership in the experiments on Maboko Island; a continuation of the Medical Entomologist's experiment in making extracts from glands and other animal parts for use in the trapping of tsetse flies; and a continuance of his work with the precipitin test.

Uganda could best carry out continued experimentation with traps against *G. palpalis* under the humid conditions of Nsadzi Island; continued trial of fats and odoriferous chemicals as attractants; trial of Carpenter pupa shelters with catching cages in their roof; an attempt, by the above means and hand-catching screens, to bring the infestation as near zero as possible on Nsadzi; the establishment on Nsadzi, or on the portion of Kimmi that is closely contiguous to

Nsadzi, of a meteorological station in conjunction with a regular fly round; and (suggested by Mr. Hancock) a good map of the Uganda section of the Lake and surveys of other *palpalis* areas in which early re-settlement is likely.

2.—CONFERENCE AT ENTEBBE ON THE WHOLE SUBJECT OF TSETSE AND TRYPANOSOMIASIS RESEARCH (ANIMAL AND HUMAN), 22ND–25TH NOVEMBER, 1933.

This conference was called by the preceding Governors' Conference to formulate a co-ordinated programme of research to be carried out by the east African territories.

The Conference was attended by Medical, Veterinary and Entomological specialists from the Belgian Congo, Nyasaland, Kenya, Tanganyika and Uganda.

It discussed and framed recommendations on a highly comprehensive programme of trypanosomiasis research, it discussed the present position of tsetse-fly research in east Africa and approved the wide programme presented, it stated its appreciation of the importance of the work being done by Dr. Maclean (in the creation, in sleeping-sickness areas, present and prospective, of settlements on economic lines) and by Dr. Corson (on the problem of *T. rhodesiense*), and it recorded additionally its appreciation of "the great practical importance of the work of the Tanganyika Tsetse Research Department to all three territories as regards the control of both animal and human trypanosomiasis."

The conference further "recorded its conviction of the need, not only for this work, but also for every facility being given by the respective Governments to continue and extend the present opportunity for personal co-operation and collaboration without regard to inter-territorial boundaries."

The proceedings and recommendations of this conference were published in 1934 under the title "Conference of Governors of British East African Territories. Research Conferences. Conference on Tsetse and Trypanosomiasis (Animal and Human) Research. Held at Entebbe, 22nd to 25th November, 1933. Nairobi. Printed by the Government Printer 1934." The recommendations of this conference were subsequently referred by the Secretary of State for the Colonies to the Tsetse Fly Committee of the Economic Advisory Council in London. That committee appointed a special "East Africa Sub-Committee" to review the whole subject. The sub-committee's report was published in 1935 as Cmd. 4951 by H.M. Stationery Office, London.

PART 9.—OTHER MATTERS OF INTEREST.

A.—VISITS RECEIVED.

During the main period (1931–34) under review visits to the work at Shinyanga have been received from His Excellency Sir Stewart Symes, Governor of the Territory, on 10th September, 1931, His Excellency Sir Harold MacMichael, Governor of the Territory, on December 7th, 1934 (when rain unfortunately prevented inspection of the work), His Excellency Mr. D. J. Jardine, Acting Governor, on 20th April, 1931, the late Sir Sydney Armitage-Smith on April 2nd, 1932, and Sir George Tomlinson on 14th February, 1934.

Amongst scientific visitors have been Prof. C. Schilling, of the Robert Koch Institute, Prof. C. Troll, of Berlin University, Geographer, Capt. H. E. Hornby, Director of Veterinary Services, Sir E. O. Teale, Director of Geological Survey, Mr. C. Gillman, Chief Engineer, Tanganyika Railways, Dr. G. Maclean, Sleeping Sickness Officer, Dr. J. F. Corson, in charge of the Trypanosomiasis Research Laboratory at Tinde. Also Dr. A. H. Owen, Director of Medical and Sanitary Services, and Mr. W. V. Harris, Assistant Entomologist, Department of Agriculture.

B.—PUBLICATIONS AND LECTURES BY THE STAFF OF THE TSETSE RESEARCH DEPARTMENT, TANGANYIKA TERRITORY, 1931–34.

1.—PUBLICATIONS.

1931.

JACKSON, C. H. N., 1931, " An Experiment on the Feeding Habits of *G. swynnertoni.*" *Bull. ent. Res.*, **22** : 175–181.

NASH, T. A. M., 1931, " The Relationship between *G. morsitans* and the Evaporation Rate." *Bull. ent. Res.*, **22** : 383–384.

PHILLIPS, JOHN, 1931, " The Biotic Community." *J. Ecol.*, **19**.

——, 1931, " Ecological Investigation in South, Central and East Africa : Outline of a Progressive Scheme." *J. Ecol.*, **19** : 474–482.

——, 1931, " A Sketch of the Floral Regions of Tanganyika Territory." *Trans. Roy. Soc. S. Africa*, **19** : 363–372.

——, 1931, " Quantitative Methods in the Study of Numbers of Terrestrial Animals in Biotic Communities." *Ecology*, **12** : 633–649.

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SCOTT, J. D., 1931, " A Practical Method of Marking Insects in Quantitative Samples taken at Regular Intervals." *S. Afr. J. Sci.*, **28** : 372–375.

1932.

[THE MEMBERS OF THE TSETSE RESEARCH DEPARTMENT], " The Work of the Tsetse Research Department of Tanganyika Territory." A reprint of articles published in the *Tanganyika Standard*, 8th October, 1932–7th January, 1933 : 1–29.

NAPIER-BAX, S., 1932, "*Notes on Anti-Tsetse Clearings.*" Government Printer, Dar-es-Salaam, 1932 : 1–15.

1933.

JACKSON, C. H. N., 1933, "On the True Density of Tsetse Flies." *J. Anim. Ecol.*, **2** : 204–209.

——, 1933, "On a Method of Marking Tsetse Flies." *J. Anim. Ecol.*, **2** : 289–290.

——, 1933, "Causes and Implications of Hunger in Tsetse Flies." *Bull. ent. Res.*, **24** : 443–482.

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NASH, T. A. M., 1933, "The Ecology of *G. morsitans* and two possible methods for its destruction." *Bull. ent. Res.*, **24** : 107–157 ; 163–195.

——, 1933, "A Statistical Analysis of the Climatic Factors Influencing the Density of Tsetse Flies, *Glossina morsitans* Westw." *J. Anim. Ecol.*, **2** : 197–203.

POTTS, W. H., 1933, "Observations on *G. morsitans* in East Africa." *Bull. ent. Res.*, **24** : 293–300.

SWYNNERTON, C. F. M., 1933, "Some Traps for Tsetse Flies." *Bull. ent. Res.*, **24** : 69–102.

1934.

BURTT, B. D., 1934, "A Botanical Reconnaissance in the Virunga Volcanoes of Kigezi, Ruanda, Kivu." *Kew Bull. Miscell. Inform.*, **1934** (4) : 145–165.

JACKSON, C. H. N., 1934, "A Note on the Concentrations of Tsetse Flies." *Bull. ent. Res.*, **25** : 457–458.

[THE MEMBERS OF THE TSETSE RESEARCH DEPARTMENT], "A Further Account of the Anti-Tsetse Campaign in Tanganyika Territory." A reprint of articles published in the *Tanganyika Standard*, 7th October, 1933–1st May, 1934 : 1–32.

SCOTT, J. D., 1934, "Ecology of Certain Plant Communities of the Central Province, Tanganyika Territory." *J. Ecol.*, **22** : 177–229.

SWYNNERTON, C. F. M., "Tsetse Work To-day and To-morrow." *Eastern Africa To-day and To-morrow*, **1934** : 77–81.

——, 1934, "Protection of Vegetation against Grass Fires as a Possible Solution for Some Tsetse Problems." *Bull. ent. Res.*, **25** : 415–30.

VICARS-HARRIS, N. H., "The Occupation of Land Reclaimed from the Tsetse Fly in Tanganyika." *East African Annual*, **1934–35** : 1–6.

2.—LECTURES.

Lecturer.	*Subject.*	*To Whom.*	*Date.*
C. F. M. SWYNNERTON.	The Problems of the Tsetse.	Imperial Institute.	1933.
——.	,,	British Medical Association Centenary Meeting, Nairobi.	1933.
B. D. BURTT.	The Tsetse and its Problems.	Zoological Club, University College of Wales, Aberystwyth.	1934.
C. H. N. JACKSON.	The Tsetse.	Musoma Native School.	1934.
——.	,,	Tabora Native School.	1934.
J. Y. MOGGRIDGE.	,,	Kiwanda Native School.	1934.

C.—THE TSETSE RESEARCH DEPARTMENT'S MUSEUM AND ZOO.

1.—THE MUSEUM.

A small museum was brought into being in 1934 in a square room with high-set windows and much wall space in the north-west bastion of the " Boma " (old German fort) at Old Shinyanga.

The exhibits comprise the following :—

Illustrations of nagana, sleeping sickness and trypanosomiasis; the various tsetses—specimens and enlarged illustrations; life-history; the ecology of the tsetses of the miombo, the dry thorn-bush and the closed plant communities (*G. morsitans*, *G. swynnertoni*, *G. pallidipes* and *G. brevipalpis* in particular):

FIG. 30.—The Zoo at Shinyanga; a glimpse into the paddock through the door of the building containing the loose-boxes.

here are shown heads of the characteristic mammals; the characteristic birds; the characteristic plants and photographs of each vegetational community; the ground-haunting birds that should come in the range of the land tsetses; the water-birds that live within reach of *G. palpalis*; the food-chain of the tsetse flies (p. 236); cases with natural vegetation and backgrounds illustrating the habits and requirements of *G. morsitans* and *G. swynnertoni*; maps and photographs illustrating methods of botanical and tsetse survey; the relations of the flies and the game; control and reclamation—parasites, traps, grass-burning, non-burning (photographs), clearing methods (actual trees and implements), discriminative clearing, settlement, erosion (photographs), occupations that bring the natives into contact with the tsetses (a

small ethnological exhibit by Wheeler); history of the work; economic crops grown by our settlers and relations of the work to the gum industry. And, as an exhibit unconnected with tsetse, animal coloration and birds friendly and harmful to man.

2.—THE ZOO.

Half the old gaol has been turned into a stable, windows brought down for more light, the floors cemented and drained and six good loose-boxes built with a central communal space. On either side a small wired-in grass paddock and in the larger of these several shade trees. The details are to Vicars-Harris's credit.

Our animals at the moment of writing this paragraph include amongst others a caracal, cheetahs, a wild dog, and, amongst ungulates, a giraffe. It is hoped to add many more species to these.

The object is to test the food preferences of the several species of tsetse in regard to as many species of vertebrate as possible, and to find out the food status, in relation to the tsetses, of each of the latter.

D.—THE RELATION OF TSETSE CONTROL TO OTHER INTERESTS.

The relation of tsetse control to veterinary and agricultural interests needs no discussion. Our object is to open up country to development, both pastoral and agricultural, and agriculture in turn helps to gain and consolidate our objective. The method of not burning the grass should be particularly helpful to agriculture. On this, p. 278 above should be seen.

The relation of tsetse control, by our methods, to erosion has been sufficiently indicated. We try to open new areas of grazing to rest and relieve those that are being destroyed, but we stipulate that the grazing of the new areas shall be so regulated that they may not also be destroyed. By attempting to arrest fly advances, we try to prevent the crushing of large populations of people and cattle into areas that are too small to hold them and in which erosion is intensively accelerated in consequence of this forced concentration.

The relation of tsetse control to forestry may be regarded as requiring discussion.

First, as regards timber trees, a cleared barrier against tsetse flies should be denuded of every conspicuous tree, but these cleared barriers constitute on the whole a very small proportion of the country and they are likely to become fewer and further between as our methods continue so to improve that we can attack larger blocks.

Our non-grass-burning method, on which we rely much for certain large stretches of country, will, over much of that country, be helpful to the regeneration of certain good species of timber trees.

This is suggested already in Shinyanga and in this connection p. 102, under *G. swynnertoni*, should be consulted. In Itundwe spot sowings of the "Mkola," *Afzelia quanzensis*, subsequently left unweeded, have been coming on well and healthily through five years of not burning the grass.

Further, we are strongly in favour of the prohibition of the cutting of certain species of value when a block of country, still holding bush, is handed, uninfested, to a tribe.

Forestry can help us in turn. It has been mentioned in another part of the present paper that when fires were excluded for forestry purposes in Nigeria

the tsetses went out too, and also that timber plantations of certain types may act as barriers to the tsetses.

Secondly as regards the trees that yield gum arabic, the genus *Acacia* supplies most of the gum that finds its way out of this Territory. In the thorn-bush areas gum-yielding acacias are found nearly throughout. The most productive species as to quantity, producing good quality also, are (here) the gall-acacias, in the Sudan and (less) here, *A. senegal.* The gall-acacias characterise the mbugas (seasonally wet open grass-lands) both in the thorn-bush and the miombo. These mbugas, then, are of special importance.

The margins of the greater mbugas (with gall-acacias) form the concentrating grounds of *G. swynnertoni*, and, in the miombo, of *G. morsitans*. These mbugas are highly important as admirable and cheaply reclaimable sites for the expansion of grazing and the relief of erosion.

It may be seen from this that there is a most close coincidence between the places that are of special interest to the collector of gum and those that are vitally bound up with the extermination of two of the most important of our tsetse flies. Map 1 should be seen for the general distribution of the main gum-habitat—the thorn-bush.

One of the chief enemies of the gum-yielding acacias is native settlement, felling all trees indiscriminately. The other is the annual grass fires, destroying the seedlings wholesale and killing innumerable grown trees.

As regards the natives, the remedy has been suggested above—prohibition of the cutting of some species.

As regards the fires—amongst our plots at Kikore * was one in an mbuga in which the growth of *Acacia formicarum* was being suppressed by the fires. The result of the exclusion of fire has been in five years a splendid little clump of these excellent gum-yielding acacias, filling the plot and contrasting with the relative treelessness both of the burned ground round and of the special control. Dense up-growth of these gall-acacias and of *A. senegal* has been brought about on much ground in Shinyanga, also by not burning the grass. Not burning is definitely the remedy so far as the roots already in the ground are concerned.

As regards the tsetse work generally as enemy and friend to the gum-acacias—where we use organised grass burning our action is definitely inimical; but it is only for a very few years, as against the indefinite period during which native burning of the grass would continue. We have in any case no wish to apply this measure to the greater mbugas, the main home of the gall-acacias.

Barrier clearings must be cleared wholly, but the vast majority of the acacias are left untouched in the blocks we thus isolate. Further, in our discriminative clearing measures in Shinyanga it has seemed that we could leave out the more valuable of the acacias. The really large mbugas, carrying the main woods of gall-acacia, are infested by the tsetses only when these woods are in contact with the fly bush proper. We reclaim these mbugas from tsetse by isolating them from the fly bush by means of a marginal clearing. Pl. 12, fig. 3, shows the broken nature of the contact of the gall-acacias of such an area with the main fly bush, and the considerable proportion of the margin that was open already and had not to be cleared.

These marginal clearings are to make the mbugas inhabitable by cattle, which, keeping grass and, therefore, the fires down, are, as is shown below, an ally of the acacias.

Our further method, for the fly bush generally, of expelling the tsetse from it

* *See* p. 32 and fig. 31 on p. 462.

by not burning the grass for some years, assists the acacias that are rooted already, as the striking results referred to above have shown.

A dilemma perhaps exists with regard to a more permanent supply. Generally speaking, if you burn the grass you burn back innumerable young acacias and fail to get a close stand. If you do not burn it you favour a dense mat of old grass, humid in the rains, and an upgrowth of thicket that is partly composed of numerous acacias, new-grown from old roots. But the survival of further newly germinated seedlings is not favoured by dense shade and high humidity.

The answer, so far as the grass mat is concerned, is, again, cattle. But these, like exclusion of fire, let woody thicket grow up. With the fires prevented, slashings, a few years apart, of the elements of the thicket that are not gum-yielding acacias would be useful. But in any case, for the purpose of tsetse control, the fires need not be kept out indefinitely.

FIG. 31.—An upgrowth of young gall-acacias (*A. formicarum*) resultant on not burning the grass for five years. This is the spot photographed by J. D. Scott at the beginning of the experiment and figured as it then was as pl. 20, figs. 5 and 6, in his paper (1934, *J. Ecol.*, **22** : 177–229). These figures should be compared.

On balance, it is certain that the benefits conferred by the tsetse work on the gum-yielding trees and the increase in the numbers of the latter that will be brought about by it will very greatly outweigh any damage our work may do.

E.—LOCUSTS AND TSETSES.

In the annual report for 1930 a belief of the Masai was mentioned to the effect that when locusts come in the tsetses disappear. This might result, temporarily, from repeated or luckily-directed defoliation, but we have seen and heard of no actual instances, though we had severe visitations of the locusts during the past four years.

Jackson has noted that the mere presence of locusts does not cause the tsetses to hide themselves. "During an experiment on *G. swynnertoni* in July–August 1931, the flies were marked daily on a fixed route. A large swarm of locusts arrived one evening and settled in the marking area. During marking the following morning they covered the vegetation, and rose in clouds at every step. The catch of *G. swynnertoni* was, however, almost exactly the same as that of the day before, which in turn was a fair average catch" (Jackson).

Vicars-Harris's observation to a similar effect was recorded on p. 42 of the annual report referred to above.

An instance, however, of great destruction of cattle by tsetse as the indirect effect of an invasion by locusts comes to hand as this report is being written and, though outside of the period dealt with, is worth recording here.

Swarms of locusts visited the Kilimatinde Plain, south-east of Manyoni, and destroyed nearly all the grazing. The native owners in consequence drove their cattle to feed in the Hika belt of *G. morsitans*, wherein grass was abundant, on which *see* p. 429 above. It is stated that not less than 70 per cent. of the very large total of animals so grazed died in consequence.

F.—THE EXPERIMENTS IN KEEPING AND WORKING CATTLE IN FLY AREAS.

" The experiments described in the Annual Report for 1930 have been concluded without necessitating any alteration of the conclusions there drawn. As a result, the herd of oxen kept at Shinyanga for carrying water for the station and various experimental purposes were subjected to regular fortnightly injections of Tartar Emetic. The cattle thus treated are able to perform the work required, and maintain health, except that towards the end of the dry season, when grazing gets poor (and, incidentally work increases, owing to the longer journeys required to fetch water), they lose condition and need extra feeding.

" A further experiment was staged to ascertain if any degree of immunity had been acquired by the beasts as a result of their prolonged contact with tsetse under regular treatment with Tartar Emetic. Seven cattle, which had been kept from 58 to 125 weeks in fly under treatment, were left untreated. These survived 20 to 60 weeks after cessation of treatment, but all died in the end. Thus, although possibly more resistant than ordinary cattle, they could not be described as immunised or premunised " (Potts).

G.—BOTANICAL WORK.

The botanical work done for other Departments in the Tanganyika Territory has fallen into three categories :—

(1) systematic, or the identification of plants submitted;

(2) instruction of officers in the diagnosis of trees and shrubs in the field from their appearance in their leafy and leafless phases; instruction in their classification into vegetational communities indicative of soil conditions; and

(3) the forwarding of dried plant collections to botanical institutions in order to further the knowledge of the flora of Tanganyika.

1.—THE IDENTIFICATION OF PLANT COLLECTIONS.

Many hundreds of plants have been identified for officers of the following Departments :—Agriculture; Forestry; Medical (Sleeping Sickness); Medical (Pathological Laboratory); and Veterinary—both in Tanganyika Territory and Kenya.

An account of the vegetation found in the *G. morsitans*-infested southern Ankole area of Uganda was prepared for the Veterinary Department of Uganda following an unofficial visit by Burtt on leave in 1930.

2.—INSTRUCTION IN THE DIAGNOSIS OF TREES AND SHRUBS.

Instruction in the field diagnosis of trees, shrubs and pasture plants has been given to officers in the following Departments :—two in the Department of

Agriculture; four in the Medical Department; three in the Veterinary Department of Tanganyika, and one in the Veterinary Department of Kenya.

3.—THE FORMATION OF HERBARIA.

Herbarium collections comprising 5,075 numbers have been presented to the Royal Botanic Gardens, Kew, and to the British Museum (Natural History); and duplicate sets of all these collections have been distributed to the Herbarium of the East African Agricultural Research Station at Amani, where a comprehensive collection of the plants of the tsetse areas will be found; also to the Herbarium of the Imperial Institute of Forestry at Oxford. Other duplicates have been forwarded to the Herbarium of the Musée Botanique at Brussels and to the Herbarium, Berlin-Dahlem. We have formed a herbarium of our own.

H.—MAN'S RIGHT TO DESTROY THE TSETSE.

Fine, slender-stemmed woods of "miombo" trees or a more open formation of flat-topped and other thorn-bearing trees, with handsome trees on the rivers, characterise the country of the tsetses. Game—single individuals, pairs, parties or herds—of numerous beautiful species graze the grass, visit the waters, and stand or lie in the shade of the trees. Birds and insects of every description are present. Man lives in scattered villages in these surroundings, cultivates, does not keep cattle, is raided by game, but, in return, hunts greatly. He retains the tsetse and, with its aid, these pleasant-seeming surroundings, by burning the grass each year. This is the first of three pictures—that produced by the scattered agriculturist and his ally the tsetse.

The wooded savannas which cover east Africa to-day are essentially the product of cultivating, grass-burning man. Few fires are lighted by nature, and fewer still can have arisen when the whole country was under the cover of the evergreen forest and deciduous thicket which evidently preceded so much of the savanna and which to-day succeeds it when we exclude the grass fires. Whether our savannas originated before the advent of man or after—perhaps many thousands of years ago in a man-settled Sahara with a moister climate than to-day—none can say. It can, however, be said with some confidence that *G. morsitans* and *G. swynnertoni*, the two tsetse species that essentially belong to savanna, owe their present distribution to man.

Man has thus added to his previous limiting agencies of war and disease a further factor to circumscribe his own distribution, activities—and misdeeds against nature. The introduction of domestic stock and the acquisition by it of its present importance as an indication of wealth will have inaugurated the habit of the stock-owning tribes of retreating before any advance of the savanna tsetse flies. Man by burning provided himself (unintentionally) with enormous areas of grazing-land, but in the act of doing so he forged a weapon that expelled him from large tracts of country when the means of using them had come.

The tsetses are the most potent preservers of the natural flora and fauna. Drive out the tsetse and the whole landscape changes. The close settlements of the pastoral agriculturists press in, very soon every tree and shrub is cut down, the ground is denuded of grass and for part of the year looks like desert, cultivation covers much of it during the rains, and during the dry season its coarse and untidy stubble adds to the ugliness of the scene that has replaced the beauties of nature. Most of the plant elements disappear—and notably the pleasant miombo trees. Others are suppressed but continue to live in their roots. The

varied birds of the bush are replaced by a few adaptable species, as the funereal bush-shrike, the chestnut-breasted glossy starling, some larks, the African pied wagtail, and, in their season, the rain-storks (*Abdimia*). The composition of the insect population is changed fundamentally and crop-destroying species increase. Scrub cattle replace the fat game animals and, annually destroying their own grazing, die in large numbers from starvation. The ground, laid bare to the winds and rains, undergoes sheet or gully erosion according to its soil and gradient and becomes more devastated yearly. Man's occupations have changed—herding replacing hunting. He is accessible to administration and, socially, materially and medically, he is better off than before, but he is destroying the country he occupies. This is the second picture—produced by the pastoral agriculturist. Tsetse and scattered agriculturist, and pastoral agriculturist, each offers us a quite different picture. Pure pastoralist, were there space to deal with him also, offers another—one (ultimately) of thicket. The exigencies of commerce, native uplift and sleeping-sickness control demand the abolition of the first and pleasantest picture. Are we to perpetuate the second?

No, nor the first. The flies have, in effect, been occupying and guarding the country until man should grow wiser in his use of it. We are wiser, or should be, than the natives, and the country is now needed for development; it is our duty to-day not to reclaim these tracts, unless, having reclaimed them, we regulate the methods of agriculture to be applied to them, and limit the numbers of cattle that shall exist in them, in such a way as to ensure that the country shall not deteriorate.

Our third picture—that of the future—should be one of pleasant cottages with fruit trees, shady groves of the native trees preserved tsetse-less and other trees planted, rotation of crops in well-manured fields, a regulated number of cattle to the square mile, grass close-grazed and improved but not destroyed, and, in places, large nature sanctuaries, judiciously chosen and "managed" (in the technical sense) for the perpetuation of the old flora and fauna and used not merely for this but for the delectation of the people, white and black.

But, in reclaiming new country, we must plan for all this from the start. It will be too late when the land is destroyed as the result of hand-to-mouth settlement methods. I do not believe that we have in the past shown fully our fitness to reclaim; but I do think I see the cloud, as yet no bigger than a man's hand, that indicates that the pleas of the apostles of anti-erosion are at last producing an impression, and that the land we reclaim in the future will be subject to regulated settlement and limitation of the numbers of its cattle.

If I am right, we are justified in continuing to reclaim—for the relief of existent erosion and the fuller development of the country.

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PART 11.—DISCUSSION OF THE PROSPECTS AND NEEDS OF THE WORK.

1.—THE PROSPECTS OF THE WORK.

I feel that, generally speaking, direct attack on the flies, *e.g.* by traps and screens, may solve particular problems, as that of *G. pallidipes* in Zululand and perhaps some of those attaching to *G. palpalis*, but that only alteration of the environment, *i.e.* the deprivation of the flies of one of their needs, is likely to be successful over large areas. Discriminative clearing, late burning and non-burning of the grass, each produces such alteration and deprivation, and all of us in the Tanganyika Tsetse Research Department feel that, in these measures, we are evolving methods which promise to be successful on a fairly wide scale. Over much country, one or other of these methods is likely to succeed unaided if it is given enough time in which to do so; but to speed up this process and, therefore, to save expense and shorten the period of risk from fires and re-growth in the case of the third method mentioned, supplementary measures must be evolved for localised application. This is the stage which we have now reached, and we are visualising actual supplementary measures. Meantime, we are continuing our search for methods—or modifications of such methods—which will be applicable to new types of country. Some have been discussed in the earlier parts of the present paper.

As regards reclamation, we are pushing ahead. Some say : " You have out-stripped regulated settlement in the areas you have reclaimed. Call a halt." This is wrong. Provided the flies are not allowed back into the country reclaimed or people admitted on wrong lines, we should push steadily and inexorably on with the big schemes embarked on and with such others as may become necessary. The organisers of settlement are waking up to the fact that there are areas awaiting their activities and that these must not be hap-hazard : this was all that was wanted. Meantime, if the tribe continues to do its part in the country shown in map 3—its part being to make the clearings which it wants and to aid in the control of the grass fires and in discriminative clearing—we believe that we can gain for it the bulk of the country that is shown in that map.

Long before we can hand this over the organisers of settlement will have decided on their methods also, and the new great area thrown open, properly settled and supervised, will be exceedingly welcome to the tribe and, as a rich new area developed, will bring in revenue to Tanganyika.

In general, provided that we obtain the added field and laboratory experimentation which we require for the better testing and the fuller evolution of our methods, we feel sanguine of success over a great deal of country and, finally, perhaps, over the whole of it.

2.—THE NEEDS OF THE WORK.

(a) Work on *G. swynnertoni.*

We have been severely cramped for some years for funds even for the programme in Shinyanga, and experiment after experiment has been vitiated through lack of sufficient isolation. It will be remembered that our staff and funds since 1931 have been 25 per cent. lower than previously. Discriminative clearing and the widening and making of full-width barrier clearings at Shinyanga are urgently required.

(b) Work on *G. morsitans*.

Owing to the accident of Shinyanga having been the first district to demand our services and to certain subsequent events, our large-scale field-experiment work has been confined to *G. swynnertoni*. We have done a great amount of research on *G. morsitans*, the most important of all the tsetses both in Tanganyika Territory and outside it, and we have ideas for its control; but we have never had the money to carry out consistently the experimental attacks on it which alone can tell us whether our ideas are well-founded and then enable us to improve on those ideas. Funds for this purpose are vital. The stations visualised are Kakoma south of Tabora, our old station at Kikore and, if that can be arranged, Abercorn in north-east Northern Rhodesia; each offers different conditions and a site for different important experiments. Among the chief methods to be tested are these :—

(1) discriminative clearing in concentration sites only, the clearing to be undertaken being at first on a very small scale, but extending till the tsetses are driven out, the whole operation being based on an intimate study of the insect's habits;
(2) organised grass-burning in country to which this is suited;
(3) non-grass-burning over a number of years with such supplementary measures as seem indicated (*see* pp. 272–280 above);
(4) early burning each year (*see* p. 279 above), for which the Abercorn country in Northern Rhodesia is particularly suitable;
(5) the exclusion at first of particular kinds of game, and then of all game, from concentration sites only; and
(6) the isolation of areas which mere season or an unfavourable year should clear of their flies, if they were cut off from areas of other vegetational types.

(c) Work on *G. pallidipes*, *G. austeni*, *G. brevipalpis*, and *G. palpalis*.

G. pallidipes permeates fully as much country as *G. morsitans* in east Africa. It is only less prominent because it appears less to man, and often, while exclusive of cattle, is present in quite small numbers. There is a grave risk that, with its different habits, this species may defeat what appear to be our most promising measures against *G. morsitans* and *G. swynnertoni*. A special entomologist (Mr. Moggridge) has been detailed to investigate this species, and it is proposed that after two years of study followed by a survey of the best areas for experiment to start field-experimentation in relation to this species also. Owing to the sparse distribution of this fly over its main areas in Tanganyika, the trapping method, so useful against concentrated *G. pallidipes* in Zululand, will not be effective in these areas, although for particular problems it will be useful, especially when used in conjunction with scent baits. These possibilities will be experimented with further, for both this fly and the others.

In the course of our work on *G. pallidipes* we shall be able to study *G. brevipalpis* and *G. austeni*, to decide on the degree and incidence of their importance, and, it is hoped, to evolve measures against them. Our work on *G. palpalis* needs completing.

(d) Experiments in not burning the grass and in discriminative clearing.

These methods of altering at small cost the environment to the disadvantage of the tsetse, on a small scale and against the one fly on which they have so far been fairly tried, are proving *most* promising; and, as the East Africa Sub-

Committee of the Tsetse Fly Committee in their recent report has urged, it is very important to push on with these experiments on a really large scale, in varied localities and against other tsetse flies also. Against *G. morsitans* (as indicated above) it is proposed that they should be tried as a start in South Tabora, at Kikore, and at Abercorn.

(e) Planting, and other supplementary, experiments.

Planting, and other, experiments for use in areas which the flies will not quickly evacuate are an essential part of the work. On a small scale and in one most unfavourable district they are in hand; but they require to be conducted under other conditions also, and they cannot be carried further without some additional assistance.

(f) Game study and game experiments.

Both game study and game experiments are very important. The preliminary stage of the experiments which are located in Shinyanga is already quite fairly advanced, but, as stated already, Harrison has more on his hands than any one man can do, and this becomes increasingly the case as the planned programme unfolds. We propose also to undertake an ecological study for the elucidation of the relations of each tsetse to each common vertebrate with which it comes into contact. This is a large task but very necessary.

(g) Experimental attempts to stop fly advances.

How to stop a fly advance without vast clearings subject to regeneration, and without settlement where potential settlement is as yet absent or doubtfully adequate, is one of the problems which we most urgently require to solve. Chance after chance of ascertaining this cheaply, where the fronts of fly advances have become constricted when about to pass between thickets, have been missed in the last few years, and it would be disastrous if we were not to be enabled to seize on the next chance offered. The present methods of opposing advances mean, we think, certain defeat sooner or later. We believe that these methods can be improved on, but we wish to experiment first. There may still be in Tanganyika two spots to-day on which a limited experiment could be laid down which would teach us a very great deal.

(h) Ecological survey and study.

Not only is a botanical map vital in relation to tsetse work, but, interpreted by anyone with real ecological knowledge and combined with a survey of soils, it is of inestimable value to agriculture and may be of use in locating mineral occurrences. A full ecological survey even of Tanganyika would, properly done, cost a good deal of money, but it is proposed to expend first a sum of a few hundred pounds which should enable us to complete the survey of the considerable proportion of the northern half of Tanganyika with which one member or another of our team is already " vegetationally " acquainted, and of situations of urgency elsewhere.

An extended ecological study of the vegetational environments of the various tsetses is contemplated also.

(i) Aerial reconnaissance.

The great usefulness of aeroplanes for botanical survey for tsetse purposes has been referred to already (*see* p. 333 above). Actually, despite the presence

of aeroplanes in Tanganyika and the fact that we have needed them badly, we have had almost to give up their use owing to the fact that the hire for their flight from Dar-es-Salaam and back has (naturally) to be paid for in addition to the cost of the flights which are actually required. If an aeroplane were attached to the Tsetse Research Department it would be in use the whole time for the study of successive problems, whether of research or reclamation, for botanical survey or for travelling.

(j) The need for additional travelling.

The more problems and sub-problems that we see, the more knowledge and ideas we gain towards the destruction of the several species of tsetse. The more travelling that in the future can be done by some of us, the more likely is our work to succeed. This entails expenditure on the actual travelling and on the person who will take the place for the time being of the person who travels.

(k) The need for adequate laboratory facilities.

Space, water, electricity—all are lacking. Essential apparatus is scanty. We have been definitely handicapped through our laboratory work lagging behind our field research (*e.g.* in the case of *G. palpalis* (*see* p. 151 above)). It is wrong that the leading organisation for research on the tsetse problem should be in this position.

(l) General.

Appreciable additional staff will be necessary for the projects referred to above, and also money for labour. Expenditure on the laboratory is necessary. Finally, a water-supply for general purposes instead of " pea-soup " from small holes, something better than hot ceiling-board housing for the white staff and, for our natives, quarters that can be kept free of spirillum, will all help the work along.

3.—SUMMARY.

Considering how small have been our annual funds for some years past, our results are promising. Without extra funds we should be greatly handicapped in making further headway. With adequate funds we can make an attack on this complex of problems which may be expected to give invaluable results.

PART 12.—GENERAL SUMMARY.*

1.—THE SCOPE OF THE PRESENT PAPER AND THE SIZE AND NATURE OF THE PROBLEM.

The present paper consists principally of an account of the work of the Tsetse Research Department in Tanganyika during the four years 1931–1934, though the events that led up to it are recapitulated. It attempts also to bring up to date our knowledge of the east African tsetse flies.

In all, nearly two-thirds of tropical Africa are infested with tsetses and fully two-thirds of Tanganyika Territory are so infested; and, as though this were not enough, the flies are steadily invading new areas. In the surrounding British territories also great areas are under infestation: the position in each is summarised on pp. 2–5 above.

2.—FINANCE, ORGANISATION, STAFF, AND THE WORK OF INDIVIDUALS.

These are described in brief on pp. 17–25 above. The effect of putting natives in responsible positions in tsetse work is also discussed (p. 25).

3.—METHODS, POLICY, AND TECHNIQUE.

The attack on the problem has been by intensive research conducted in co-operation with large-scale experimental attack in the field—or so-called experimental reclamation. It has also been mainly on ecological lines, *i.e.* we study intensively the environmental requirements of each species of tsetse with a view to depriving it of the minimum requirement, most cheaply removed or modified, on which at some season or in one kind of year it depends. Team work has been the method.

The policy of the Tsetse Research Department is attack, not retirement into the fastnesses of concentrated settlement. Such settlements are the best emergency solution of the sleeping-sickness problem at present, but to develop the country to the utmost, to give the population full scope for its rightful prosperity, and to transform its herds of cattle from a wasteful and destructive incubus into a thriving and profitable asset, we can be content with nothing less than the ultimate extirpation of the tsetse through the whole of the Tanganyika Territory and eventually throughout the continent of Africa.

Advances in research technique since my annual report for 1930 include the extended use of aeroplanes for tsetse reconnaissance and of aerial photography in tsetse fly survey; the use of special "bait-screens" for drawing out those tsetses which are unwilling to show themselves to man; a method of estimating the actual populations of tsetses and the various aspects of their behaviour which overcomes the difficulty caused by their varying "activity"; hunger-staging and the use of the torsion balance (the latter suggested by Buxton) in the investigation of their physiological condition; and new methods of vegetational, faunal, and tsetse survey in the field.

In 1935 weighing of the flies in the field, on capture and each recapture, was added to hunger-staging, with results which were confirmatory and valuable as

* The table of contents should be consulted in conjunction with this summary.

regards utilisation of vegetation types and influence of season. The true population of tsetse in a rectangle of country undivided from the main belt surrounding it was regularly estimated, and the influence of factors, physical and biotic, thereby assessed, since the rate of diffusion proved calculable.

4.—DISTRIBUTION OF THE MAIN PLANT AND ANIMAL COMMUNITIES, AND OF THE VARIOUS SPECIES OF TSETSE.

(map 1.)

The two main savanna communities of Tanganyika are the dry thorn-bush or nyika (*Acacia–Commiphora*) and the taller, more uniform miombo woodland (*Isoberlinia–Brachystegia*). The nyika mainly occupies the northern part of the Territory, entering from the Sudan and Somaliland, through Kenya; the miombo comes in from the south, and dwindles out at our northern border both on the east and west.

The more characteristic large animals of the miombo are the sable antelope, Lichtenstein's hartebeest and Sharpe's steinbuck. Those of the nyika are the oryx, the lesser kudu (in thicket), Coke's hartebeest, the gazelles and the ostrich. The principal distribution, geographical and ecological, of the game animals is shown in map 7.

G. morsitans characterises the miombo, but also inhabits types of thorn-bush in Bukoba and southern Uganda, under a higher rainfall, and (in the countries south of Tanganyika) the mopane (*Copaifera mopane*). *G. pallidipes* overlaps much of this *morsitans* country.

The tsetse of the nyika is *G. swynnertoni*; its range is widely overlapped also by that of *G. pallidipes*. *G. longipennis* lives in the drier parts of this thorn-bush. *G. swynnertoni* occurs across much of the northern third of Tanganyika and is invading Kenya Colony. The two flies last named (*G. pallidipes* and *G. longipennis*) infest most of the eastern, lower-lying portion of Kenya.

G. brevipalpis, *G. fuscipleuris* and *G. austeni* are tsetses which are based on dense wooding—often associated with high rainfall, but sometimes with subsoil moisture. *G. austeni* occurs through the coastal belt of east Africa, back to the edge of the central plateau. *G. brevipalpis* is found in the same area but re-occurs also in the region of the lakes. *G. fuscipleuris* is found near the southern Kenya border and across it and in localities in Uganda.

G. palpalis is mainly a water-side tsetse. It is almost entirely confined, in Tanganyika Territory, to the shores of the Lakes Victoria and Tanganyika. In Uganda and Kenya it extends far along the main rivers that flow into or out of the lakes.

5.—CONCURRENCE OF REQUIREMENTS.

The most important general point discovered by us is that each species seems to need a concurrence of different vegetational types. Thus, within a general fly belt of any one species, the tsetses occur in numbers only about the meeting-points of two or more vegetational types. Each of these types is necessary to supply a different requirement of the flies—for example, the conditions necessary for mating, breeding, feeding, or sheltering, from lethal degrees of heat or desiccation, or from enemies, during rest. If therefore any essential type is rendered unsuitable by destruction or mere modification, the tsetse, it would seem, must go.

6.—THE ECOLOGY AND THE IMPORTANCE OF THE VARIOUS SPECIES OF TSETSE.

The ecological and economic importance of each of the various tsetses may be summarised as follows :—

(a) *Glossina morsitans* Westwood.

(i) Suitable and unsuitable vegetational conditions.

While *G. morsitans* is essentially the miombo tsetse, being unable to live in the thorn-bush except in regions of high rainfall, it may filter into the thorn-bush for some miles at its contact with the miombo and be particularly abundant at the contact. It is also absent from open plains, evergreen forest, continuous deciduous thicket in sufficient width or in leaf, and, seasonally, pure *Combretum* savanna. It is exceedingly scarce seasonally or permanently in much of the more homogeneous miombo itself.

The miombo is generally dominated by *Isoberlinia globiflora*, with which are mixed a number of species of *Brachystegia* as well as other tree-genera. The grass growth varies from good to exceedingly poor. The associated soil is eluvial, but the general miombo is dissected by alluvial drainage valleys that support acacias and other characteristic trees, as well as anthill thickets large or small. Large alluvial enclaves are fairly frequent, and out in these—though not in their margins—flies are scarce, whether the enclaves be open or clothed with the drier types of thorn-bush.

(ii) Needs as regards concurrence of requirements.

A concurrence of vegetation types appears definitely necessary to *G. morsitans*. The small glades intersecting the miombo, and the edges of the greater mbugas (*see* appendix 1), open or with gall-acacia, are used by this tsetse as feeding-grounds. To these flies resort with the onset of hunger from the miombo proper or other more sheltered type which forms the home. Large thicketed termite heaps, topped by big trees, may represent the home at some seasons, though surrounded by alluvial soil. The home comprises both rest-haunt and breeding-ground, and its " furniture " consists of fallen logs, hollows between the root-bases of trees, rot-holes in the trunk and other dark nooks in which the flies rest and in which the females deposit their larvae. Other non-classical sites—"bad" sites—are proving to be used for this purpose quite largely, but, still, within the home.

Within the home few young flies, females, or hungry flies appear to man—though it is there that the larvae are deposited and the young flies emerge. The flies seen in the " home " are almost entirely non-hungry, and are for the most part loitering males on the look out for females. The latter are there but in hiding.

(iii) The physical factors.

G. morsitans occurs from near sea-level up to an altitude of 5,500 feet. The mean rainfall in the areas in which it occurs varies from about 27 to 40 inches annually.

A study of the physical factors showed that insolation and air temperature, wind and drought are all less severe in the miombo, used as the home, than in the neighbouring alluvial areas, in which visibility is of course better, and which are therefore more suited for the detection of prey, and, which both for this reason and because hungry flies will brave unpleasant conditions, are resorted to, as stated, as feeding-grounds.

During the dry season, with a rising evaporation rate, the hunger of the flies rises, and towards the end of the season, with drought conditions severe, the numbers of flies taken on transect rounds fall to a low point. Throughout the year a correlation (with a lag) was found to exist at Kikore between fly numbers and the evaporation rate, the correlation being negative with the evaporation rate when it was above an optimum zone, and positive when below it.

A suggestion that the low temperatures which occur in June and July, also kill the older flies in the field, still needs confirmation.

Consequent on the rise in hunger in the dry season, there is a rise in the numbers of the flies in the feeding-grounds relatively to the numbers in the home, provided that the feeding-grounds themselves are not too exposed to the fierce isolation of this season. In the wettest months the feeding-grounds are used less.

The effect of the normal grass fires is to accentuate the severity of the physical conditions of the dry season, which are unfavourable to *G. morsitans* except in picked spots. Fierce, organised fires, still hardly tested on *G. morsitans*, may be found to have a more immediate and marked effect.

Breeding (deposition of larvae) appears to be favoured by dry weather in the field, as it is in the laboratory.

The early rains and the short dry season following these offer ideal conditions for the flies and the fly population, from its minimum point of the year, soars upward. As the country dries after the second or long rains, density temporarily rises again.

The effect of abnormally heavy rains seems to depend on the type of country. They favour increase of *G. morsitans* in dry, well-drained regions and its decrease in ill-drained, low-lying areas. The distribution as well as the amount of the rainfall is, however, extremely important. A continuous deluge over days in the second-named type of country in the season 1929–30 produced wholesale destruction of the flies.

(iv) Seasonal concentration and shifting.

G. morsitans in much of its range concentrates in the dry season in and alongside portions of the drainage valleys, and spreads again through the great areas of deciduous miombo in the rains. While such concentrations—which are distinct from feeding-grounds but contain them—have been observed in Tanganyika in the Tabora belt, no instance has yet been recorded of the flies having spread thence in large numbers during the wet season.

(v) Cover-control possibilities.

In some widespread types of miombo it is likely that the exclusion of grass fires may be effective against this fly, through the complete alteration in the vegetational and resultant physical conditions which it brings about. The results obtained from a small experiment in Kondoa–Irangi already support this view. Cover-control by discriminative clearing is also expected to produce important results.

(vi) Mating organisation.

The well-fed males of *G. morsitans* accompany man and other animals as a following swarm, to pounce upon any female which may attack the latter in order to feed. The loitering of the males in the breeding-grounds has been mentioned already. Paths and open patches of ground are also a rendezvous of the sexes.

(vii) Economic importance of *G. morsitans*.

G. morsitans carries very effectively the Rhodesian type of human sleeping sickness in addition to nagana of cattle. It is of very wide distribution, being found over very large areas in every east African colony except Somaliland, Kenya, and Zululand. Fully half of Tanganyika is infested by it. It is the most important, economically, of the east African tsetses. At the least its importance equals that of *G. pallidipes*.

(b) *Glossina swynnertoni* Austen.

(i) Suitable and unsuitable vegetational conditions.

G. swynnertoni is absent from evergreen forest, from the great areas of miombo (*Isoberlinia–Brachystegia*) woodland, from continuous thicket, and from very open tree savanna and open plain; also apparently, in Musoma, from country where there are scattered thickets without higher trees.

This species is found in the nyika or dry thorn-bush (*Acacia–Commiphora–*other genera) throughout the areas of its occurrence; it is invading new country of this type, and has apparently great possible fields for conquest still before it.

(ii) Needs as regards concurrence of requirements.

It has sometimes proved difficult to dissociate the home from the feeding-grounds of this tsetse. However, the wooding of the eluvial soils, unmodified by a substratum of limonite crust, is definitely a home, and true feeding-grounds have been located and proved in a variety of more open situations, including the edges of mbugas.

Very commonly, as occasionally with *G. morsitans* also, the home and feeding-ground types are so combined as to be indistinguishable. The flies are in effect, in these cases, living at their feeding-ground all the time, the necessary home vegetation and furniture being there also.

Breeding, in thickets and under rocks, occurs in the home. The furniture of the breeding-ground consists in the bases of many-stemmed thicket shrubs, lianas lying near the ground and fallen or leaning trunks, especially in thicket; and overhanging rocks.

(iii) The physical factors.

This fly occurs up to 6,000 feet and the range of rainfall in the areas in which it is found varies from about 16 inches to 30. The country in which it occurs is liable to intense desiccation during the late dry season and generally is much drier than that inhabited by *G. morsitans*.

Like *G. morsitans*, *G. swynnertoni* decreases greatly towards the end of the dry season, the decrease being accelerated by the effect of the annual fires. The peak numbers occur in the break between the earlier and later rains, and at the start of the long dry season.

Hunger and female percentage are lowest just after the break of the first or early rains.

There is evidence that reduction in numbers due to reclamation of any kind, or the burning out of thickets on well-grassed eluvial soils supporting *Commiphora Fischeri* and *Ostryoderris*, has led, in Shinyanga, to a more marked concentration on the hard-pan drainage strips, where thickets persist on these. After the fires in Shinyanga, thickets tend to persist on the short-grassed alluvial hard-pans more than on the eluvial, being protected by the poor burning of the surrounding grass. If these thickets are cleared, the fires have a more marked effect on the tsetses.

(iv) Seasonal concentration and shifting.

The flies become much less numerous in the late dry season in areas devoid of thicket. Recent study of the fly rounds points to the conclusion that there is a seasonal shift of the main fly population to different types of vegetation in turn. Observations in 1935 suggest a change with the seasons in the types of breeding-place most in use and the possibility therefore of attack on one season's breeding-places only.

(v) Cover control possibilities.

The effect of prohibiting grass fires altogether is to bring down very greatly both fly numbers appearing to man and the actual population of *G. swynnertoni*—apparently by preventing recovery from the low level normally reached each year at the end of the long dry season. The country, in Shinyanga, thickens up much more rapidly than does the miombo inhabited by *G. morsitans*, but a heavy fall in the density of the flies, following the exclusion of grass fires, precedes this formation of thicket. The subject is under close study.

Cover control by means of discriminative clearing is producing great effects in Shinyanga.

(vi) Mating organisation.

The males of *G. swynnertoni*, like those of *G. morsitans*, form " following swarms " seeking females. These swarms attend man as well as other animals. The habit of concentrating on hard-pan strips assists also in the meeting of the sexes.

(vii) Economic importance of *G. swynnertoni.*

This species, like *G. morsitans*, is a highly efficient carrier of the Rhodesian form of human sleeping sickness, and is equally exclusive of cattle. It is distributed in extensive belts over the north of Tanganyika, from Shinyanga, Musoma and Mkalama nearly to Moshi. It has also invaded Kenya Colony and could, it is thought, infest much of it.

(c) *Glossina pallidipes* Austen.

(i) Suitable and unsuitable vegetational conditions.

Short of real desert, treeless grass-land, and the depths of extensive rain forest, no type of savanna vegetation appears unsuited to *G. pallidipes* provided good thicket is present. River-fringing thicket or forest is especially suitable. The range of *G. pallidipes* in east Africa is hardly surpassed even by that of *G. morsitans.*

(ii) Needs as regards concurrence of requirements.

G. pallidipes bases itself on thicket and may even to some distance penetrate heavy evergreen thicket, using it as a rest-haunt. It breeds not only in thicket but also like *G. morsitans*, under logs and tree-bases in the more open savanna outside. Its main feeding-grounds are in the tree-savanna, which, with the glades, margins of open spaces, large and small, the margins of its thickets, and roads, it scours for animals. An instance of a miniature " belt " of this fly, complete in the smallest of spaces, is given.

The " furniture " of the breeding-ground is much the same as for *G. austeni* (*q.v.*), but rocks have not been seen to be used appreciably and the mere shaded leaf and humus bed of the thicket is much used even away from closely overhanging objects. A semi-herbaceous bed of a three-foot-high *Justicia* was found to contain many pupae.

(iii) The physical factors.

The standard climate varies from that of the hot, moist, equatorial coast, to that of the semi-desert climate of parts of the Voi region, to that at 6,000 feet in Mbulu and to climates in latitudes in which the freezing-point is annually reached. Atmometer readings indicative of the evaporative power of the air through the year in the rest-haunts and feeding-grounds of *G. swynnertoni* in one of its drier habitats are given in the section dealing with that species on p. 98. These apply there to *G. pallidipes* also.

G. pallidipes rarely comes to our traps in the heat of the day, though days on which calf-bait was used afforded some exception. This tsetse becomes hungry and appears more to man in the late dry season.

(iv) Seasonal concentration and shifting.

Very definite dry-season concentration has been recorded from Zululand, Portuguese East Africa, and Tanganyika Territory. Conversely, our investigations of Mpapwa in both wet season and dry, showed that the riverine forest, the main haunt of this fly in the late dry season, was in the wet season deserted for drier thicket.

(v) Cover control possibilities.

Late organised fires, affecting cover, have certainly rendered country in Shinyanga less suitable for this fly in the course of some years of burning. On the other hand, its general population has increased in areas that are burned, but not fiercely. What the ultimate effect of changing the vegetation to a denser type by not burning the grass at all will be, by itself, on this species we cannot yet tell. Reinforced by planting to produce an unbroken, dense, stand, it will certainly prove useful.

The modification of cover by discriminative clearing is likely to be useful, and, at Mpapwa in Tanganyika as well as at Melsetter in Southern Rhodesia, the placing of mere cleared barriers across river valleys appears to have checked seasonal invasions.

(vi) Mating organisation.

Over much of its range this species is sparse, but that it is capable even in these conditions of collecting together and mating is suggested by observations in which several flies—up to a dozen—have attacked simultaneously in country in which, in between, no flies or an odd fly were seen. The blood of man is not a favourite food and no following swarm forms at man.

(vii) Economic importance of *G. pallidipes*.

For a discussion of this question the abbreviated summary given on pp. 111 and 112 with the discussion thereafter of the economic position of the species should be read.

(d) *Glossina austeni* Newstead

(i) Suitable and unsuitable vegetational conditions.

This species does not inhabit the interior of unbroken rain forest of wide extent, savanna wooding that is without thicket, or open country.

It is found both on alluvial and on eluvial soils and even on steep mountain slopes. It favours on the whole secondary thickets in the dry season of more or less evergreen type, and thickets of a type intermediate between this and rain forest. Plantations of Ceara rubber with shrub undergrowth are used freely.

(ii) Needs as regards concurrence of requirements.

Dense to fairly dense cover appears best suited to form the rest-haunt and breeding-ground. Interspersion with more open vegetational types seems important and the break-up of rain forest into patches lets this fly in. The more open elements must be used as feeding-grounds as most attacks have taken place outside thickets; but in two or three cases, where bush-pigs had found regular sleeping and rootling places or were abundant otherwise in strips of thick forest *G. austeni* appeared to have concentrated there.

The furniture of the breeding-haunt consists in the usual logs, tree-bases, rocks and lianas, in most cases under close canopy.

This fly rarely appears to man but it comes to bait-cattle, and the female percentage thus appearing is exceptionally high, being from 40 to 100 per cent.

(iii) The physical factors.

G. austeni occurs from coast-level to 3,000 feet (north of Kilosa), under the range of general climates thus indicated. Figures are extracted from some of Moreau's observations to suggest something of the conditions *G. austeni* may experience in one of its eco-climates. The fact that attack may take place outside of thicket at any time of the day suggests a drought tolerance perhaps approaching that of *G. pallidipes* and surpassing that of *G. brevipalpis*, but some evidence suggests that it does not wander far from its thicket base as *G. pallidipes* does.

(iv) Seasonal concentration and shifting.

On these points little is known. Wallace thought he noted some contraction of range when the rains had given place to odd showers. Little also is known yet of the mating organisation or of the chances of attacking this species by cover control, except, as regards the former, that no following swarm forms on man.

(v) Economic importance of *G. austeni*.

G. austeni rarely attacks man, and it is therefore probably of no importance in relation to sleeping sickness. Its relation to cattle disease is uncertain, but it attacks cattle readily, and its reputation in Jubaland is particularly bad. It occurs apparently in suitable localities in the whole coastal strip right back to the central plateau, and may prove of the utmost importance.

For further details the brief summary and the statement regarding its economic position on p. 124 should be seen.

(e) *Glossina palpalis* (Rob.-Desv.).

(i) Investigations carried out by the Tsetse Research Department.

Riamugasire (Mugasiro) Island, Musoma, was chosen for studies in the bionomics of this fly and for the experimental release against it of a parasite, *Syntomosphyrum glossinae* (March 1933–November 1934). Maboko Island, Kisumu, was used for the trial of trapping against *G. palpalis* (October 1932 onwards).

(ii) Suitable and unsuitable vegetational conditions.

G. palpalis occurs normally near water—*i.e.* rivers and lakes—but under special conditions it may be found as much as a mile away. The following types of country are avoided by it:—forest fronted by lake-shore clearings; forest of the densest type; extensive xerophytic thicket; open savanna woodland; the back of large belts of papyrus unless intersected by crocodile passages.

G. palpalis is never found far from woody or at least rank herb-vegetation as well as water. It also occurs in strips of closed forest or thicket following rivers and streams.

(iii) Needs as regards concurrence of requirements.

At least two types of vegetation are required—viz. light and heavy. The rest-haunt is in massive wooding (Fiske's term) which may be rain forest or lighter but closed vegetation of *Anisophylla* and other tall shrubs. Feeding-haunts are found in open situations along the shore-line, at fords, on rivers, or at regular haunts of animals in suitable wooding up to some distance back from the shore. Hungry flies range over open water, also to a certain distance from the shore as rock and canoe catches showed.

Breeding may occur in either type—on the beaches if shrubs are present—or strongly in places quite away from the water and rest-haunt even in xerophytic vegetation (Maboko), where, however, the flies hardly appear to man. The furniture of the breeding-haunt may be much the same as was described for *G. morsitans* and *G. swynnertoni* or—a very favourite site—may be the shaded sand of the fly beaches.

G. palpalis feeds mainly on crocodiles and monitor lizards, and freely, if they are present in its haunts, on tortoises and large mammals. It feeds sometimes also on birds. The reptiles mentioned are preferred to man. Bait-screens are more attacked than is man alone.

(iv) The physical factors.

Under the conditions found on Riamugasire Island, flies become active at temperatures above 73° F., and may be maximally active at about 79° F.; but there is some suggestion that saturation deficits of about ·40 inches discourage activity. Activity is also inhibited by winds of a speed over 7 or 8 m.p.h., and is almost always lower in the afternoons irrespective of conditions. C. W. Chorley found an agreement between activity and types of cloud.

In April 1933, an unusually hot month, numbers and hunger were higher than at any other time. Mathematical estimation of the total tsetse population of the island, however, showed that flies were not appreciably more *active* then than at any other time—the actual population being very high. During the two warm, wet months which followed, apparent density, hunger, and actual population fell to low levels and never rose greatly again. Young flies were most numerous when the apparent density was highest or was starting to decline.

Crocodiles were breeding and at their maximum about July; though their numbers rose greatly at such times there was no correlation at all with the hunger of the tsetse.

Where a high female percentage in the old flies is observed in one *place* as compared with another, this does not coincide with high hunger on the part of the males unless it is multiplied by the male density. This supported the suggestion, since dropped, that females fear to show themselves where eager males are too numerous. In time, however, as opposed to place, there is a simple agreement between female percentage in the old flies and high hunger on the part of the males.

Pupae were taken in greatest numbers in the drier months. There was a suggestion that this might be due to concentration of breeding-sites owing to leaf-fall.

Male flies did not generally live more than 7 weeks. Longevity was apparently greater in drier weather—possibly with feeds sufficiently frequent.

Despite all the above and in particular the non-coincidence of high hunger-rate with high saturation deficit, the months characterised by the latter and, alternatively, high temperature, saw the tsetse numbers at their lowest. The lethal effect, if any, seemed not to be through hunger, as is the case for *G. morsitans.*

(v) Seasonal concentration and shifting.

On the mainland, with its higher seasonal desiccation, seasonal concentration is more marked. On the Kuja river there is dry-season contraction down from the smaller tributaries. " Along the Sudan–Uganda border there is a very definite wet- and dry-season expansion and shrinkage of the fly distribution " (Carpenter, letter).

(vi) Cover control.

Neither grass burning nor its prevention can be employed as measures against this tsetse, which lives mostly where fires do not come. Cover-control by discriminative clearing is a possibility. Long-shore clearing is definitely effective, and experiments projected will show to what extent this can be further reduced.

(vii) Mating organisation.

The non-hungry males await the arrival of females in places which the latter must pass. They do not follow man in swarms for the interception of females, as do the males of other species, but they form these following swarms on reptiles and antelopes.

(viii) Economic importance of *G. palpalis*.

G. palpalis is of little importance to cattle. Its distribution, though locally restricted, is wide in central and west Africa, and it has decimated large human populations in the past through infection with the *gambiense* type of sleeping sickness. This disease continues endemic in many parts, and there is always the risk of larger outbreaks.

The generally linear distribution of *G. palpalis* offers hope of its control. Traps, hand-catching off screens, and discriminative clearing are the measures being tried against it. For a fuller discussion of these methods the summary on p. 159 should, however, be seen.

(f) *Glossina brevipalpis* Newstead.

(i) Suitable and unsuitable vegetational conditions.

G. brevipalpis does not occur where thickets are absent or generally light in character. Where the thickets are heavy and either numerous or riverine it may inhabit either thorn-bush or miombo. It also occurs freely, like *G. austeni*, in the rear of retreating rain forest where this has become broken up, and it is found in great numbers based on abandoned and overgrown Ceara rubber plantations.

(ii) Needs as regards concurrence of requirements.

The breeding-place and rest-haunt are in thicket. The species, however, comes out into the more open savanna at sunset and is found settling freely on paths. There is also evidence to show that it hunts the open country by moonlight as well, or that at least it then accompanies hippopotami in their wanderings. Like *G. austeni*, however, it appears capable of finding all its needs fulfilled where a thicket-haunting animal such as the bush-pig frequents

regularly one spot inside thicket for sleeping and rootling. In rubber plantations it was mainly found for a short distance back, only, from the margin.

The breeding "furniture" consists of low-coiling lianas, the bases of massed thicket stems, tree-bases, fallen trunks and even mere leaf-litter, but these must always be under good shade.

At bait-cattle fewer females are taken than in the case of *G. austeni*. Out of a total of 947 taken near Amani 23·4% were females. The figure in the same locality for *G. austeni* was 56·2%. The species comes little to man and was not attracted by screens. It attacks bait-oxen readily.

(iii) The physical factors.

The elevation varies from sea-level to, probably, 4,500 feet. This suggests that the temperature range and the rainfall range is fairly wide also. Some indication is given of the eco-climate prevailing inside a type of forest that is probably on the borderland of suitability and unsuitability for this species at the high end of its humidity range.

As regards humidity and temperature the Box and Cox relation between *G. brevipalpis* and some of the other tsetses (as *G. palpalis*) is noted, these latter hunting mainly by daylight and *G. brevipalpis* probably largely by night. That it will not face conditions of low humidity is suggested also by some of its other habits. On Maboko, however, dry days sometimes forced the species to attack, when on wet days it could only be found by searching the tree-trunks.

(iv) Seasonal concentration and shifting.

This has definitely been noted, as has (fairly far south, lat. 20) an apparent avoidance of large rivers in the cold months.

(v) Cover control possibilities.

Areas have been seen in which fierce grass burning should greatly reduce the thickets and drive *G. brevipalpis* away. Where the thickets are heavier it would not. The possibility of control by not burning is discussed, but experimentation is required.

(vi) Mating organisation.

The queues of male flies found outside the thickets on paths are evidently, to judge from what happens when females appear, for the purpose of meeting the latter.

(vii) Economic importance of *G. brevipalpis*.

The summary given on p. 170 and the discussion that follows regarding the economic status of the species should be seen.

(g) *Glossina fuscipleuris* Austen.

(i) Vegetational habitat and needs as regards concurrence of requirements.

Forest more or less dense, and thick vegetation (presumably woody) are recorded as the base of this species, and are doubtless used as rest-haunt and breeding-ground; but it attacks also freely in the open—even in an open maize-field—and, from the recorded observations, it uses the more open country, as well as the drinking places of animals, as feeding-grounds.

(ii) The physical factors.

The indications obtained in regard to the physical factors, together with the short summary given on p. 173 and the note following it on

" economic importance " should be seen. Observations on this species so far are limited.

(h) *Glossina fusca* (Walker).

It would seem that this species is not unlike *G. brevipalpis* in its habits and habitat, but that on the whole it bases itself on heavier forest. Its feeding-grounds are paths, roads, and contacts of heavy vegetation, with light. Under certain climatic conditions, it bases itself on lighter vegetation in the dry season than in the wet.

This species would appear to have practically no economic importance in east Africa, owing to the very limited areas that it occupies.

(i) *Glossina longipennis* Corti.

No work has yet been done by the Tsetse Research Department on this species. A note is given on p. 175.

7.—LABORATORY EXPERIMENTS.

(a) Experiments on pupae.

The approximate mean weights in milligrams of the pupae of the several species of tsetse used were :—

G. austeni, 21; *G. swynnertoni*, 27; *G. morsitans*, 30; *G. pallidipes*, 31: but the weights of the pupae obtained by breeding were appreciably less than those of pupae brought in from the field. Buoyancy tests and weighing were, both of them, useful to determine viability. The viability of pupae weighing under 15 mgms. was so small that they were not worth using in experiment.

The pupae (*e.g.* of *G. morsitans*) from parents kept under high temperature were light, and died in far greater numbers than pupae from parents kept under lower temperatures.

Flies (*G. swynnertoni*) emerging from pupae deposited by parents living in the dry season were lighter than the offspring of parents living in the late rainy season.

The pupal period varied with the mean temperature but not with the diurnal range. In cold weather *G. morsitans* took as much as 72 days to emerge; the males took longer than the females. The variation produced by experiment was from 20 days to 2½ months. In 1935 two pupae marked in the field and revisited took more than 92 days to emerge.

Each extreme has its disadvantages. At 23 days (temperature 86° F.) the deaths were doubled as compared with the deaths in the control at 45·5 days. Pupae kept at 87·8° F. (*G. swynnertoni*) showed a 20-day period but gave rise to flies which failed to survive. On the other hand, pupae lose weight all the time, so that those existing at very low temperatures, and so with a long pupal period, are liable (*a*) to mortality from this cause and (*b*) to give rise to flies which will be unable to survive, as well as (*c*) being exposed themselves to more prolonged general risks.

A temperature of 87·8° F., if maintained, is therefore effectively lethal, as is exposure to 102–104° F. for 3 hours, or 111–113° F. for half an hour. Similar results were obtained with *G. morsitans* pupae exposed in surface soil in the field, the pupae succumbing as soon as the soil temperature reached 113° F. At a depth of two inches a soil-surface temperature of 110° F. did not affect them. At 1½ inches a maximum surface temperature of 119° F. killed them.

Maximal soil-surface temperatures over 110° F. are general in Shinyanga for many months, and over 102° F. for nearly the whole of the year. Therefore, adequate thinning of breeding-cover should result in wholesale loss. Roughly, during the rains, at least three consecutive fine days are needed to kill unshaded pupae in nature, but in the dry season most would not survive one day.

The parasite *Thyridanthrax abruptus*, however, survived temperatures even of 119° F., where it was present within the exposed pupae—which may be a useful fact.

G. morsitans pupae can withstand 104° F., if administered in daily doses of two hours to a total of as much as 10–12 hours. Pupae newly formed or nearing emergence are especially delicate and easily killed by high temperatures.

Freezing (32° F.) for 24 hours had but little effect on emergence, and for 1–1½ hours no effect on emergence at all.

Humidity did not affect the pupal period in the experiments carried out by Potts and by Buxton and Lewis, and it minimised the chance of survival of *G. morsitans* and *G. swynnertoni* only towards the lethal end of the temperature scale. Buxton and Lewis have found that low humidity strongly increased the tendency to mortality in *G. tachinoides* but in *G. submorsitans* only when it descended to 11% at 66° F. Loss in weight resulted from lowered humidity and this loss was proportional to the saturation deficit.

The lethal period for pupae submerged in water, or water-logged soil or sand, was four days. Occlusion of the so-called respiratory lobes was not fatal.

(b) Experiments on adults.

Adult *G. morsitans* do not survive one hour at 104° F., but repeated short exposures are not fatal. They survive freezing (32° F.) for exposures up to 12 hours, but there was a suggestion that digestion might have been adversely affected by the freezing.

Adult *G. morsitans* survived short exposures at 104° F. even when repeated many times (Potts), and there is evidence in nature (Swynnerton, Nash) to show that the fly population in open places is constantly changing, the individuals doubtless returning to shade.

High temperature with low humidity appears unfavourable to the flies of the *morsitans* group in the field. Nash found that moderate evaporation—medium humidity—in the field was followed by high fly density. Buxton and Lewis found that under conditions of high humidity at 86° F. *G. tachinoides* and *G. submorsitans* died quickly.

Potts found that the females of *G. morsitans* and *G. swynnertoni* at temperatures unstated survived high humidities well, but there was a steady if a light increase in longevity with decrease in relative humidity per cent.; twenty appears to be the optimum percentage for *G. morsitans*. Flies of the *G. morsitans* group reproduced best under the driest conditions tried—unnaturally low humidities (Potts, 20%, *cf.* Buxton and Lewis, 11%).

Dry conditions decreased the survival period of young unfed flies. The effect of a meal in increasing survival was most marked—and very marked—under the driest conditions. The flies with a meal survived at high temperature combined with high humidity for a shorter time than at high temperature and medium humidities.

Two batches of *G. austeni* at 20% humidity and 77·7° F. gave a mean survival period of 2·3 days unfed and 2·5 days fed (human blood), whilst two

similar batches at 100% relative humidity at the same temperature, fed, each had a mean survival period of 7·7 days.

Buxton and Lewis have noted that there is very little difference in the survival of fed and unfed flies at high humidities, but at lower humidities fed flies live much longer, presumably because they have greater reserves. Both hunger stages and weight bear a relation to the fat content of the flies.

In " wild " flies, the fat decreases as water is lost. The percentage of water in the total non-fatty weight is maintained nearly constant at about 70 in every stage of hunger. In young (unfed) flies it is higher at about 74%. It follows that the percentage of water in the gross weight *including fat* varies with the stages of hunger, from about 58% in hunger-stage II to 70% in young flies.

Buxton and Lewis have pointed out that the tsetses are amongst the insects that possess the power of compensating for evaporation by metabolising fat and so producing additional water. The exhaustion of the fat would thus, failing food, be followed by exhaustion of water and death, but each new feed renews the fat-bodies and with them the potential moisture supply.

The laboratory experiments on the effects on the various species of tsetse of varying combinations of meteorological conditions, and including those concerned with the determination of the variations in weight and fat-and-water content of flies kept under varying conditions and coming from different areas, have continued in 1935. Jackson has carried laboratory methods into the field in a most useful manner.

(c) Limitations of laboratory work.

Laboratory-bred flies, like laboratory pupae, are lighter and have a lower fat percentage than wild flies. They also lose weight more rapidly than do flies in the field.

In addition, the fat-cycle in captivity is quite abnormal, and flies of the *morsitans* group in the laboratory appear to undergo an abnormal and accelerated hunger cycle. Laboratory flies also do not produce nearly enough pupae to maintain their numbers, though the percentage of viable pupae is satisfactorily high.

The blood used (mainly sheep) may have been relatively unfavourable. It is possible also that constant conditions of temperature and humidity may be unfavourable to tsetses. The possible effect of the conditions of close confinement and prescribed food on an insect so active naturally and so selective of its food and its surroundings from moment to moment, must be considered as well. More work is necessary, therefore, before we can say that the results thus obtained are in all ways reliable, and all findings in the laboratory must be confirmed, where possible, in the field. At the same time this method, of which Buxton has been the protagonist, is already giving valuable clues.

(d) Lessons drawn from laboratory work.

The main lessons so far, drawn both by ourselves and by Buxton and Lewis, are that the flies in the laboratory fail to survive conditions which we are producing in the field by means of our discriminative clearing, and that far less than wholesale clearing may, therefore, actually exterminate them.

8.—TSETSE FLIES IN RELATION TO THEIR FOOD.

(a) General.

The tsetse may be attacked in some cases by control of its food supply. An appreciable beginning has been made with the study of this subject.

It is important to know what its whole food supply is. It has been claimed that *G. pallidipes* feeds on the latex of *Euphorbia tirucalli*. This, however, has been disproved by us, for that species and for *G. swynnertoni* and *G. morsitans*. It would seem that blood supplies the whole food of the tsetse.

A crocodile was lassoed and flies fed on it and newly shot crocodiles were tested. Blood flowed even from the top of the head and the membrane between the "scales" of the back. In nature if the crocodile is swimming the flies cluster especially on the crest of the head.

The different species of tsetse come in contact with different food animals. *G. morsitans* and *G. swynnertoni* feed mainly on the ungulates of the savanna, *G. palpalis* on reptiles and the tsetses of the heavy thickets (*G. brevipalpis*, *G. austeni* and often *G. pallidipes*), on bush-pig (probably especially) and other dense-wooding species.

Quite inconspicuous animals such as snakes and monitor lizards in cover are found and attacked.

(b) Favoured and favourable foods.

Tsetse have preferences as between different food animals. Thus *G. morsitans*, *G. swynnertoni*, *G. pallidipes*, *G. brevipalpis* and *G. austeni* attack cattle more readily than man and man more readily than goats, while *G. palpalis* attacks heavily crocodiles, monitor lizards, and tortoises when it is leaving man unmolested. Other instances of such preferences are given.

Preferences for individual food animals of the same species have also been shown.

The preference for cattle as against man is far more marked in some species of tsetse than in others. Some seldom attack man at all.

Some kinds of blood are more *favourable* than others. Thus *G. morsitans* produces fewer pupae when fed on goat's blood than when feeding on ox blood.

All flies once fed on a cheetah preferred death to a second feed. On the other hand, flies thrive on a "hunting dog" (*Lycaon pictus*), but, so far, have failed to breed.

Intolerance of attack and a dense hair cover are probably inconducive to successful attack.

Cercopithecus monkeys succumb to trypanosomiasis, yet thrive in thick "fly." This may be a matter of intolerance purely, or of being a less-favoured food.

Such preferences and special protections may be of the greatest importance should attempts be made to control tsetse by attacking its food animals.

(c) Sight *versus* scent.

Knowledge of the senses by which the flies find their food is important. Eyes of tsetse flies of three species sent to Dr. H. Eltringham for examination led him to suggest that, while differing so little from eyes of ordinary flies that there was no reason to suspect special acuity of vision, they are probably adapted for detection of movement as distinguished from that of form. The further suggestion was made that its habits may have developed in the tsetse the tendency to use its eyes more than other flies do.*

An experiment involving 3,000 *G. morsitans* suggested that this species hunts mainly or entirely by sight. However, there is a good deal of evidence to suggest that *G. pallidipes* may be attracted by scent even from some little

* Dr. Eltringham wrote on 6.i.36 that these suggestions must be regarded as highly provisional only as he is now submitting the subject to a much fuller investigation. The results of this have now been published (1936, *Trans. R. ent. Soc. Lond.* **85**: 281–288).

distance; the addition of certain gland extracts to bait the traps set for *G. palpalis* resulted in increased attraction to and increased catches by the treated traps; and it may be surmised that *G. brevipalpis*, hunting by night, hardly does so by sight alone. It may be that while sight, developed by use as Eltringham more generally suggests, is the main sense used by some species for hunting their food; in others, though their eyes are similar, scent plays a strong part. These experiments are being continued on *G. morsitans* and *G. swynnertoni*.

(d) Relation to game.

It is sometimes assumed that tsetses follow game herds about. Tsetse do not live in continual association with such herds. They feed, and fly off to digest their meal; meanwhile the animals may move on and next time the flies are hungry fresh food must be sought.

Part of the mechanism by which they discover game was brought to light by an experiment. A concentration of the flies was produced in the absence of a game-concentration by hoeing paths converging to a pool. No concentration formed at a second pool close by, to which paths were not hoed. Hungry tsetse haunt strongly roads and paths.

It was also found that flies thus concentrating do not finally disperse till some time after the game has left. This observation will account for some of the instances in which flies have been found without game. It has, nevertheless, been noted repeatedly by us that a very small game population indeed, at any rate of regular habits, can support a fair fly population.

An examination of the relations of the flies to the mammals, small and large, and to the ground-birds, suggests that there is no mammalian group which even approaches the ungulates in importance as food for the woodland tsetses. There is some evidence that tsetses will use the blood of birds to a greater extent when mammals are absent.

Owing apparently to increased hunger, due to a heightened evaporative power of the air, the numbers of *G. morsitans* fall throughout the late dry season, although in most of the places studied the game animals increase and also become more readily available within the areas still infested at that season. Evidently high density of game does not avail to prevent the annual fall in numbers. The increase of hungry flies in the tsetse feeding-grounds occurs in the dry season independently of the number of game animals using those places, but in close association with the meteorological changes. The latter factor is very much more important than that of a larger or smaller game supply.

A given game population *just* adequate to support a very few tsetses is theoretically adequate to support a number many times larger: the animals will not be drained of blood and they may be found as easily by many flies as by few. But their habits must be sufficiently normal and regular to enable them to be readily found.

The question of tolerance on the part of the game animals will, however, have to be taken into account. Observations suggest also that an exceptionally high game density—or cattle density—may permit tsetses to live in country somewhat more open than they could otherwise inhabit.

In other cases, in Tanganyika, cattle seem to have been of benefit to the tsetses in another way also, by helping to spread them.

The probable relations of the tsetse to the nocturnal mammals are discussed. Tsetses, with the probable exception of *G. brevipalpis*, are not usually nocturnal, but under particular conditions they may make use of animals during the night or of night animals during the day.

(e) The effect of the Great Rinderpest on the tsetses.

An analysis of the evidence on the effect of the Great Rinderpest on the tsetse leads to the conclusion that it was probably partly responsible for the abandonment of certain areas by the flies.

This happened, however, without the destruction of more than a proportion of the food animals. Again, in some belts in which the susceptible animals were destroyed, recession did not occur. It is believed that, where it did so occur, there were probably in each case other contributing factors.

At dry-season foci of the flies, the rinderpest may also have had the effect of driving out the game generally by the concentration on the surviving species of great numbers of flies, following on the death and dispersion of the susceptible and perhaps favoured species. Or the flies on the wing may have been slow to adapt themselves to new species of food animals. Of this possibility, some small amount of confirmatory evidence exists.

(f) The effect of game control.

It has proved possible in Rhodesia to bring about a sufficient destruction of the game animals, in savanna wooding of miombo in a strip, 10–20 miles wide, between fences, to push *G. morsitans* back—the surviving animals having become nocturnal; but, generally speaking, this can be done adequately only under European supervision and organisation and, for great areas, is costly; further, unless the treated areas are surrounded by barriers against the reincursion both of flies and of game, the measure must go on indefinitely. Unsupervised native hunting is likely to be quite ineffective.

Though undoubtedly useful against *G. morsitans* under certain quite widespread conditions, yet under more widespread conditions in our Territory, it is not believed that attack on the game will exterminate this species. Nor will it exterminate *G. pallidipes*, *G. austeni*, or *G. brevipalpis* in the thick cover on which they are usually based, or *G. swynnertoni* in the thicketed country in which it is usually found. In the case of *G. swynnertoni* the situation found in Maswa in 1922 suggested that with natives present in sufficient numbers *G. swynnertoni* may make good on man even if the game is greatly reduced.

For further discussion of this subject, the summing up on p. 228 should be seen.

9.—TSETSE FLIES IN RELATION TO THEIR ENEMIES.

The main known enemies of the tsetse are sixteen or seventeen species of parasitoids that lay their eggs in the tsetse pupae, which are then eaten out by the resultant parasitoid larvae.

There is evidence that the pupae are devoured also by insects and by such mammals as elephant shrews and mongooses, perhaps also by ground-scratching birds. Thus 3·1% of about 5,000 empty puparia of *G. palpalis* showed signs of insect predator (not parasitoid) attack and numerous pupae were so fragmentary that no diagnosis was possible. Evidence that predator attack may be of importance in the case of the pupae of *G. morsitans* was added to in 1935.

Predators on adult tsetse include dragonflies, robber-flies (Asilidae), wasps (*Bembex*), spiders, and birds. The species of the latter which have been seen to attack tsetse are drongos, fly-catchers and bee-eaters. The birds that specially and carefully search bark and twigs are also probably of importance.

Spiders of various bark-haunting species of Salticidae that leap on their prey are believed to be formidable enemies of the resting female tsetse. Natives sometimes ascribe widespread disappearances of tsetse to " plagues " of robber-

flies or dragonflies. Those of the Sesse Islands that are heavily infested with web-spiders in most cases have few *G. palpalis.*

The habit of the female tsetse of choosing grooves or surfaces of the same colour as itself to settle on, by suggesting a need for concealment argues the existence of enemies.

Birds tend to concentrate their attack on those species which, of their normal and preferred food, are at the moment most abundant and available, but to leave them in favour of other and equally palatable species where these become easier to find. These latter species then act as buffers for the protection of the others. Attack on the tsetses is thus probably fluctuating in nature.

Some of the predators prey on others of the predators, as is seen in the "chain of attack" deduced from observations.

10.—A MAN-MADE FLY BELT.

The Tanga–Korogwe belt provides an instance, in which the fly belt has extended as the rain forest has been broken up and driven back by the natives, and in which the three species present—*G. pallidipes*, *G. austeni* and *G. brevipalis*—are based on rubber and *Cassia* plantations. Man is, however, very generally responsible for the present distribution of the tsetses in east Africa.

11.—BALANCE IN TSETSE POPULATIONS.

A preliminary discussion of this subject is included in the present paper in order to provoke discussion and work on what is an important practical question.

12.—EXPERIMENTS IN DIRECT ATTACK ON TSETSES.

(a) Attack by parasites and fungoid diseases.

By suitable technique, the pupal parasitoid of tsetse, *Syntomosphyrum glossinae* can be bred and released in the field very cheaply at the rate of millions monthly.

Unfortunately *Syntomosphyrum* has poor burrowing powers and cannot reach the majority of *G. morsitans* pupae buried in light sandy soil without humus.

The result of a large experiment with *Syntomosphyrum* against *G. morsitans* resulted only in the raising of the parasitisation rate over a hill-side full of breeding-places to 12% of the total tsetse pupae that were present.

On Riamugasire Island in Musoma, however, *G. palpalis* breeds in almost pure humus. It was therefore determined to try the effect of the parasite there.

The work was started in 1933. After early difficulties, large releases of the parasite were made, up to half a million monthly.

A release of 519,000 in one month resulted in a parasitisation of only 5% of the *G. palpalis* pupae on the island,.and, throughout the experiment, up to late in 1934, the results were similarly disappointing.

The fundamental difficulty was ultimately found to be that saturated air is fatal to this parasite, and that the air in the interstices of the humus, even where the latter was dry, was always near saturation.

A fungus found to be affecting the tsetses has offered little hope, as atmospheric conditions which are more than ordinarily wet must be continuously maintained in order to make it pathogenic and to bring about its general spread.

In any case biological control, though often helpful in reducing "agricultural" pests, is unlikely to be of use against tsetse, which in most cases must be exterminated completely. There are exceptions to this necessity, as in Zululand, where the mere drastic reduction of fly density in a game reserve should result in there being but few wandering flies to infect cattle in the surrounding areas.

(b) Attack with bait-screens on the feeding-grounds of the tsetses.

An attack was made on *G. swynnertoni*, in a block of country in Shinyanga, by hand-catching off cloth screens, which increase the catch of females. The screens were carried by pairs of catchers, who worked daily at the feeding-grounds of the flies. The latter were much reduced but the experiment failed, partly because of constant re-infestation across the "barrier" clearing, partly through the difficulty of enticing out the last of the females.

The screens thus used are also attractive to *G. palpalis*, *G. morsitans*, and *G. pallidipes*, raising in every case both the total numbers and the percentage of old females in the catch; and they are much used in our reconnaissances. They appear to be unattractive to *G. brevipalpis*.

(c) Tsetse traps.

Traps, more or less effective, of over twenty kinds have been evolved. These include the AS (awning screen trap) (pl. 2, fig. 3) which is very effective against *G. palpalis* and *G. pallidipes*, the revolving drum trap (pl. 2, fig. 5, pl. 3, fig. 1) effective against any fly that settles on the drum, and the animal traps (pl. 2, fig. 6, and pl. 3, fig. 3).

The animal traps contain a protected and concealed live animal and, evidently through scent, have been very effective in catching large numbers of *G. pallidipes*. Scents in the form of gland extracts from animals, placed as bait in the AS. screen traps have added much to the catch of *G. palpalis* (C. B. Symes). There is a definite observation also that animals passing near a trap increase the catch.

In addition Blunt has evolved a "sailing" trap which moves continuously to and fro on a long wire in moderate breezes, and Chorley in Uganda has produced a form of the crinoline trap adapted to the catching of tsetse. An electric trap has been made that can be attached to a lorry or the back of a train.

Traps consisting of a single log, simulating natural logs under which pupae are deposited, were made cheaply on the lines devised by Carpenter and Lamborn and later improved by ourselves. The pupae deposited are killed by exposure to sunlight by rolling the covering log to one side every three weeks. It has been estimated that thirty shillings' worth of such traps would dispose, in an area only moderately thickly infested by *G. morsitans*, of 43,200 pupae annually.

During trapping with the AS (SS) trap on the Ngongho river in Shinyanga in 1932, 17,162 *G. pallidipes* were caught between the end of August and the end of November. The local population of the species is a small one and subsequent trapping has not been equally effective, though *G. pallidipes* continues to be present, doubtless in smaller numbers.

An experiment is being carried out on Maboko Island with the same trap against *G. palpalis*.

Traps will certainly bring density down where it is high in the case of *G. palpalis* and *G. pallidipes*, though not in that of *G. swynnertoni* and quite

insufficiently in that of *G. morsitans*, but, at the best, flies will persist in much lowered density. In a very few cases (*e.g.* probably Zululand) less than complete extermination will suffice to solve a local problem. In most extermination is needed.

A reason for the fact that traps for adult tsetse are unlikely to exterminate them is that flies of the *morsitans* group are taken in negligible numbers in and after the two wet seasons, and *G. palpalis* (on the islands) in low numbers in the drier weather. The effective trapping season in both cases lasts for only three or four months in the year. This has been found to apply to the Harris traps tried here as well as to our own. Further, the present indications on Maboko are very much to the effect that, by selective elimination of the individuals that come readily to our traps, we are producing a strain of *G. palpalis* that will not go into traps.

13.—INDIRECT ATTACK ON TSETSES BY MODIFICATION OF COVER.

(a) Complete clearing.

Complete clearing is objectionable on the grounds of expense and of the erosion ultimately caused. Progressive eating into the margin of a fly belt is wrong also, on the last-named ground.

(b) Attack by mere isolation.

The cutting-off of gall-acacia savanna from the true " fly bush " is effective. The wandering flies on the wrong side of the barrier clearing are isolated and die out. Gall-acacia savanna is by no means the only type of wooding which can be so isolated and freed of tsetse. A scheme is under consideration for freeing a great shelf of ground in the Yaida (Mbulu) country of seasonal infestation by interposing a barrier between. It is proposed also to isolate experimentally a large uniform area of miombo in order to prevent its wet-season infestation, and it is proposed further in attacking a concentration of *G. morsitans* to interpose a barrier between its sites and alternative unoccupied sites.

(c) Discriminative methods.

(i) *Discriminative clearing.*

Discriminative clearing—that is to say either complete or partial clearing of concentration sites, or the removing of certain elements only from these or from wider areas—promises to be very useful, judged by the striking effect of work of this kind on *G. swynnertoni* in Shinyanga. Much is hoped from experiments on *G. morsitans* that are in prospect. Thus in South Tabora one finds apparently useful concentration sites occupied only when a particular vegetational inter-zone type is present in them.

Burtt's work at Mpapwa suggested a form of this method of attack for *G. pallidipes* and its immediate result was successful.

An experiment in removing merely the " furniture " from a rest-haunt and breeding-ground of *G. brevipalpis* produced the local expulsion of this fly. The blocking-up or burning of individual natural breeding-sites or mixing the earth in them with some cheap chemical deleterious to the pupae or repugnant to the female tsetse have been suggested. The vast numbers of separate sites normally available put such methods out of count except in very limited breeding concentrations, seasonal (*cf.* p. 268 above) or otherwise.

For the limitations of the general measure, pp. 268–270 should be read. During 1935 in Shinyanga our experiments in discriminative clearing were

interrupted owing to the impossibility of obtaining labour—the natives having received so much money for their crops that there was no incentive to work.

(ii) *Discriminative clearing, and consolidation of clearing, by ungulates.*

The enlistment of ungulate mammals for the suppression of regenerative growth has been considered. The results obtained by placing a few hundred goats in a small clearing proved disappointing: the goats seemed to need the competition of cattle, eating the herbage, to force them to concentrate on the regenerating tree shoots.

The sitatunga antelopes (*Limnotragus spekei*) so increased on the Sesse Islands after the removal thence of the population in about 1910 that they completely cleared up both the herbage and the undergrowth, to the very great detriment of the tsetse, *G. palpalis* (*see* figs. 19 and 20).

(iii) *Discriminative settlement.*

Discriminative settlement—the placing of new settlements in the sites of tsetse concentrations—is also promising. At Selya in Kondoa district a settlement so placed resulted in the destruction as such of an important fly feeding-ground despite the continuance in the papyrus alongside of residence by a herd of buffalo. Fuller experiments are hoped for, and it is suggested that sleeping-sickness settlements placed thus, if the soil is good and water is provided, might contribute to the destruction of a fly belt. The sites require expert selection from the point of view of tsetse control.

(iv) *Prohibition of burning and planting.*

Prohibition of grass burning, tried against *G. swynnertoni*, seems most promising and may exterminate it. The conditions are radically altered in the direction of densification of cover, but the effect on the flies is more rapid than this seems to explain. What exactly brings down the numbers of the flies so soon is being investigated.

A smaller experiment against *G. morsitans* has been similarly promising and it is to be tried against this species, as already on *G. swynnertoni*, on a much larger scale. It is at the same time realised that there are great areas of country in which it will certainly be ineffective. Certain difficulties are, in any case, met with, but supplementary measures have been devised. Support is essential: a most promising and important experiment, in which fly density had already been brought down, had to be abandoned in 1935.

It is possible that in some places it may be sufficient merely to prohibit burning in certain limited sites important to the tsetses.

Discriminative planting may prove necessary in order to thicken up places, at certain points in the whole area treated, which mere non-burning leaves insufficiently affected. Shrubs and trees that survive the conditions and spread themselves freely naturally are under trial for this. Other means of attacking such refractory enclaves have been devised and are being or will be tried—as, for example, clearing localised settlement, temporary local exclusion of food animals.

Very early burning each year is likely under certain conditions to produce sufficient vegetational densification to lead to the expulsion of *G. morsitans*.

(v) *Discriminative planting.*

Possibly the planting of the hard-pan strips referred to above as a measure supplementary to not burning the grass will suffice by itself.

14.—INDIRECT ATTACK ON TSETSES THROUGH THEIR FOOD SUPPLY.

An experiment is in progress in Shinyanga (*G. pallidipes* and *G. swynnertoni*) to ascertain the effect on the tsetse of disturbing the habits of the game animals, of various degrees of reduction, and ultimately if necessary of expelling them from a piece of country—in so far as this may be feasible.

For the above experiments different blocks of country have been set aside—two for the experiments, two as sanctuaries. These blocks have been accurately mapped to show in detail the distribution of the vegetation, and the population of all species of game animals is regularly assessed day by day. The usual routine observations on the tsetse are carried out in addition.

"Management" (*see* appendix 1) will be applied both for the expulsion and attraction of the game—the former to reduce the shooting.

The work was begun early in 1934 and will take several years to complete. A great deal of very interesting and relevant information on the habits of the animals is meantime being obtained by means of the technique we are evolving. The preferences of the flies are being studied as well—there may be other species besides cheetah on which they cannot live.

Similar experiments, but confined to dry-season concentrations, are planned for *G. morsitans*.

15.—INDIRECT ATTACK ON *G. MORSITANS* BY THE INTRODUCTION OF HUMAN ACTIVITIES.

The mere presence in some degree of man and his activities appears to repel *G. morsitans*, even though the bush is not destroyed at all fully or the game animals seriously reduced in numbers. This is dealt with on p. 325. It does not apply to *G. swynnertoni* and *G. pallidipes*, nor, probably, everywhere, to *G. morsitans*, but it may explain how, although game and bush were not exterminated and the rinderpest had not yet arrived, *G. morsitans* disappeared from those of its belts in the Transvaal that were settled.

16.—COMBINED DIRECT AND INDIRECT ATTACK ON TSETSES.

Organised grass burning late in the season combines direct and indirect attack on the tsetse. The flies are driven across a cleared barrier, the breeding and refuge thickets are mostly burned out except beside the rivers and on hard-pan, where the fires cannot fully assail them, many pupae are killed, and the conditions of desiccation that are brought about and continue up to the rains are very trying to the flies that remain.

The general effect, in Shinyanga, has been to drive flies out of well-grassed country and a proportion of them on to unburned or poorly-burned patches of ground, thicketed or open wooded, met on the way. Fly numbers are considerably reduced in any case, but to make the measure completely effective, the poorly-grassed, badly-burning patches are cleared.

A successful technique has been developed for holding the grass unburned until a suitable moment comes; usually early in September.

In sparsely-thicketed blocks, or in a block cleared of thickets by hand (Block 1 at Shinyanga) or cleared effectively by the fire (Block 6), the expulsion of the tsetse has been accomplished in from one to four years. Burning postponed for two years is more effective than annual late burning.

The measure is applicable only to country that carries a sufficiently continuous grass-growth and not so much intractable thicket that its removal is uneconomic.

Locusts, by destroying the grass, may prevent a good burn.

17.—EXPERIMENTS FOR THE PRODUCTION OF AN ABSOLUTE FLY BARRIER.

(a) Dispersal of tsetse flies.

Dispersal of the tsetse flies may take place by any of the following means :—Carriage by cars and trains, carriage by man, and spontaneous movement along man's paths, carriage on cattle and movement along cattle paths, carriage by game. Flies may also be spread as the result of ill-directed hunting, and as the result of ill-directed grass fires. Dispersal may also be automatic and unaided, in the latter case owing to seasonal expansion as a promoter of colonisation of new centres and further expansion thence. However, spread, automatic and unaided, largely or wholly as the result of recurrent hunger, is regarded as by far the most important factor in dispersion.

(b) The width of clearing which the flies will cross.

Experiments to determine the width of open country which the flies will cross unaided are described.

An 800-yards clearing was quite insufficient to prevent the spontaneous crossing of the flies. Of marked flies one in every 233 was found to cross a 1,200-yard clearing. None was recovered across a 1,400-yard clearing, but another time of year and greater density of flies might have produced evidence of crossing here also. Probably no clearing less than two miles in width will suffice as a permanent barrier even against uncarried flies.

The effectiveness of the clearing was dependent partly on whether odd trees were left in it. These facilitate crossing by the flies. The reason for crossing is that the flies are ranging for food.

Experiments have also been made regarding the width of country which *G. swynnertoni* will cross on man, on man and cattle together, and on cattle alone (the latter, in the experiments, representing game).

Man proved a more dangerous carrier of the flies than cattle. The flies mostly fed quickly on the latter and left them.

(c) The width of clearing which will safeguard a road.

It was concluded that flies (*G. swynnertoni*) seldom fly out to attack objects for a greater distance than 200 yards over level ground, but that, if the range of vision of the flies is increased by a concave contour of the ground, the range of attack will increase, it may be, to 400 yards. A road clearing, that is, should be 600 yards wide at least.

A road running along the middle of a perfect 1,200-yard clearing was kept fairly infested by movement of people joining on native paths from the fly bush. This, and often, pieces of ground, re-infested, again lost their flies when the human traffic was subjected to being de-flied by a picket. Settlement of a clearing, previously freed of flies, has been noted to produce re-infestation by *G. swynnertoni*, for, as was concluded from Moggridge's experiments, the flies travel much more readily on man than on four-footed animals, seeing that they less readily feed on him.

Some rules as regards clearings have been formulated.

(d) The efficacy of a thicket as a barrier to *G. morsitans* and *G. swynnertoni*.

(i) *Investigation of natural thicket.*

An investigation of the efficacy of thicket as a barrier against *G. morsitans* was conducted at Kazikazi (pl. 15, fig. 1) from July 1931 to October 1933, and

experiments in the formation of thicket and the testing of likely species of trees and shrubs for the purpose have been carried out in Shinyanga and at Itundwe in Kondoa–Irangi.

Four semi-clearings, simulating savanna wooding, were made 50, 100, 400 and 900 yards in width respectively, inside the thicket, and catches were carried out daily. Traverses were made through the unbroken thicket. Catches were made on elephant paths. Numerous flies were marked and catching was carried out for their recapture on either side of a mile-wide thicket neck.

During the leafless season the flies were found in the thicket in small numbers, becoming smaller and smaller the further the thicket was entered. Very few usually were taken in the clearing 900 yards in.

It was concluded that a thicket of the Itigi type, rather open below, and with a high fly density beside it, requires in the leafless season as a minimum to be somewhat more than one mile wide, in order to prevent odd flies from drifting through it in numbers such as might found a colony beyond.

The following conclusions were reached.

Game was abundant in the thicket. Flies were carried into the thicket by man and presumably by game. They probably entered it also in limited numbers spontaneously when it was leafless.

They did not fly over the thicket. They entered it and drifted about in it.

During the leafy period it was almost impossible to find a fly in the thicket. This leafy period comprised the wet season and part of the dry, and the deduction was that an evergreen thicket would be effective in narrow width all the year round.

(ii) *Thicket produced by cessation of grass burning and by planting.*

Deciduous thickets have been formed by us cheaply in some kinds of country by keeping the grass unburned in a strip running between two fire-breaks. A road protected by a thicket of this type in Shinyanga that is only 300 yards wide, keeps nearly free of flies, but to prevent all possibility of passage, it would be wise to give a real barrier strip, if deciduous, a width of three or four miles. A wide strip is nearly as cheap to form by not burning the grass as a narrow one.

An evergreen thicket would have to be planted. Our planted evergreen barrier of manyara (*Euphorbia tirucalli*) in Shinyanga, though only 100 yards wide, possessing some flaws and freely passed by game, is keeping a road remarkably well protected from infestation.

This *Euphorbia* is ideal for the purpose in the dry climate of Shinyanga, and every cutting planted in the dry season grows, but the species is not of economic value.

Under relatively favourable planting conditions, such as obtained in most *morsitans* areas, plants of economic value could be used. The various species of *Cupressus* and *Callitris* form good dense cover through the long persistence of their lower branches and would be perfect for the purpose. They would require to be planted in an area in which they could be profitably exploited when grown.

In Shinyanga *Cupressus* and *Callitris* failed through drought. At Itundwe both *Cupressus arizonica* and *Callitris* have succeeded, though (purposely) left unweeded.

An evergreen thicket will probably be useful as a relatively narrow fringe on the edge of a deciduous thicket and may enable the whole width to be reduced. A fringe even of deciduous thicket along the edge of a clearing is regarded as similarly useful.

Any Territory that is prepared to afforest and has a *morsitans* advance to

deal with would be well-advised to consider whether it cannot combine the two objects. The future inter-connection between tsetse control and forestry is likely to be exceedingly close.

(e) Human activities as a fly barrier.

The effect of human activities on *G. morsitans* has been referred to on p. 494 of this summary. They have been effective in barring a fly advance in Nyasaland without serious extermination either of woodland or game. How they have done it and the conditions under which they will do it need fuller investigation.

(f) Other types of fly barrier.

The Southern Rhodesian fly barrier is discussed on p. 454. Water, escarpments, and a vertical wall as barriers are discussed on pp. 326 and 327.

(g) Game barriers.

Our experiments with game fences of different kinds are discussed on pp. 328 and 329.

18.—SURVEY.

(a) Air survey.

About 80 square miles of the Shinyanga country have been photographed from the air, as a contribution to the botanical surveys which are part of our investigation of the tsetse. Numerous visual reconnaissance flights have been made over the surrounding chiefdoms and districts for assistance in the formulation of reclamation schemes.

The Central Province from Kazikazi to Singida and between Singida and Kondoa was reconnoitred in the same way. The objects here were the selection of barrier lines, should any seem suitable, against several tsetse advances, the appreciation of the extent of the danger, the determination of the country that could still be invaded and the general survey of the great blocks of tsetse-excluding Itigi thicket further west.

On four or five flights in the areas last named, sketch-maps were made and work accomplished which on foot or by any other method could not have been carried out in less than two years in this very impassable country—*see* map 6. In addition, the sites for our experiments regarding the passage of thicket by tsetse were readily selected from the air (pl. 20, fig. 2).

Other flights have also been made in connection with the problem, and the very great value of air reconnaissance to the tsetse work has been demonstrated.

(b) Surveys made on foot or by car.

Considerably over 100 surveys, reconnaissances, and visits of inspection and advice, including those round Shinyanga, were carried out by members of the Department in no less than 53 areas up to the end of 1934. The accounts of a few only of them are summarised below.

In addition, in 1935, surveys were carried out by us in Western Mwanza (Saragura Area), Karagwe, Singida, Morogoro, Kondoa–Irangi, Mbulu, Uvinza and a part of the Masai steppe.

(i) *The situation in Musoma.*

A tsetse survey of much of the Musoma district was carried out at the request (South Mara) of the Sleeping Sickness Officer and (North Mara) of the Administration. No measures were recommended in the north; in the south

a bridge of bush, likely to let *G. swynnertoni* into uninfested country, was cut on our recommendation. Banagi in the same district was visited and the fly situation seen there was noted.

(ii) *The Gigoma situation near Kahama.*

A shallow drainage line clothed in mbuga wooding crosses diagonally as a band a great space more or less open that is nearly surrounded by miombo. The mbuga remains infested through the contact of its ends with the latter, and the remedy proposed has been to detach it by clearing across these ends.

(iii) *The problem at Mpapwa.*

The Mtambi river system, with tributaries flowing in from a long-standing infestation further east, approaches the veterinary headquarters at Kikombo (Mpapwa). A western tributary traverses the veterinary farm at Tubugwe. Cases of trypanosomiasis occurred in the Tubugwe herd; in one year there were no less than 60. Cases followed at Kikombo itself.

Investigation suggested that the tsetse infestation (*G. pallidipes*) was attached in the dry season to the dense, evergreen riverine wooding, and that it was at that time concentrated specially at the watering-places of the cattle; but that it receded during the rains when grass and humidity were high. It was recommended therefore that clearings should be made across the riverine strips to check the seasonal advance. This was done and the cases of nagana have almost entirely or completely ceased.

It was interesting that even before the clearings were made the cattle could be protected from attack to a considerable extent by watering them in the heat of the day, when *G. pallidipes* did not appear.

(iv) *The Loskitu (Sikitok) problem in north-west Handeni.*

G. pallidipes, coming in from the Pangani river in the north, had apparently succeeded during seasonal spread from a streamlet ten miles away in colonising permanently a minute area (400 yards square) of semi-riverine wooding on the west side of Loskitu hill. The seasonal spread from this centre in turn precluded the cattle of the Wakwavi from using the waters of the mountain and deprived them of valuable grazing.

The clearing of the new fly colony was recommended and carried out, with, it is believed, complete success.

(v) *The Handeni problem.*

The natives—Wanguu and Wazigua, the latter particularly—are liable to recurrent famines. The suggestion was made that concentration of the population should take place in selected sites with rich soil and water, both to avoid these famines and to provide against the possibility of the arrival of sleeping sickness in the future.

A tsetse survey was carried out and indicated that a great part of Uzigua, from which it was proposed to move the people, was little infested with tsetse. Also that the infestation in Nguu (of *G. morsitans* and a few *G. pallidipes*) was very much higher, but that it could probably be banished from any piece of country selected for settlement by settling the river valleys only. It was also a country in much of which the tsetse could probably be extirpated merely by not burning the grass. The effect on our measures of a sparse sprinkling here and there of *G. pallidipes* was uncertain.

(vi) *The Mkwaja problem in relation to* G. pallidipes.

This was typical of the instances in which the fact that the waters alone are infested precludes the use of grazing. The clearing of the waters was recommended.

(vii) *The Tabora–Nzega–Kahama problem.*

The object was to select sites for research on *G. morsitans*, and for experimental reclamation against it in a more typical area than those previously studied in the Central Province. The sites were eventually selected south and south-east of Tabora, with headquarters at a spot called Kakoma.

(viii) *An extended reconnaissance for the selection of a site for work on* G. pallidipes.

Moggridge visited Nindo in western Shinyanga, Moshi (the Rau rain forest), some country between the Pare mountains and the Tanga–Moshi railway and, then, eastern Usambara. While much interesting observational work was conducted on *G. pallipides* and other tsetses, no suitable site for prolonged research on this species was found, flies being everywhere too scarce. Finally Kilifi in Kenya was chosen.

19.—RECLAMATION.

(a) General.

The scheme laid down in 1923–24 suffered some interruption in 1929–30, but has since been resumed and developed. Both tribal and hired labour have been employed on a great scale. The Department, in the four years here dealt with, has spent in Shinyanga £995 on tribal labour and £2,715 in all on work beneficial to the natives, not including salaries of Europeans. The contribution of the native authorities in the same period was £156.

In every case the site of the clearing has been selected and the work marked out, organised and supervised by ourselves. The co-operative spirit of all—Tribe, Administration and others—has been good, and it is only by such co-operation combined with expert guidance that a broad scheme, such as this is, can be carried out with success.

An extension also of our co-operation to Kwimba, Maswa, Mwanza, Musoma, Nzega, Kahama, Mbulu and Kondoa has once more taken place during this period. The whole of the clearings—66 in all—carried out by ourselves or by the tribes under our recommendation and supervision are listed in table 56. (Details as regards object, method of clearing, number of man-days, and cost are given on pp. 358–361 above.)

(b) The year 1931.

1931 was a poor year for labour as the tribesmen had to fight locusts. 1932 saw the real resumption of the work, the re-growth of which may be seen from the following figures :—

In 1931	1,578	tribesmen in Shinyanga worked 10 days.
„ 1932	5,442	„ „ „ „ „ „
„ 1933	10,163	„ „ „ „ „ „
„ 1934	13,098	„ „ „ „ „ „

(c) The year 1932.

Two great results were attained in 1932. These were the conquest of Chibe, the traditional headquarters of this section of the tribe—an event which gave

rise to rejoicing—and the completion of the Beda corridor for the safe passage of cattle to the great Huruhuru Plains : for both *see* map 1.

In Maswa in 1932 the large Marialuguru salient was cut off from the main fly belt with a view to freeing it of tsetse.

(d) The year 1933.

In 1933 the out-turn of the tribesmen and the spirit shown by them was most satisfactory, and this was particularly so in view of the fact that this was not a district which was making its first great effort, but one in which reclamation work had been in progress for nine years already.

Additional work was done on the Beda corridor, the proposed corridor from the southern Shinyanga chiefdoms was carried into the bush for three miles on a width of two, most of the gall-acacia wooding of the south-east Huruhuru Plains system was isolated by means of a barrier clearing from the fly bush proper which kept it infested, water-conservation work was carried out here and a corridor was made, with a minimum of work, into the mbuga system of the Manonga. Many thousands of cattle have grazed there regularly since. Clearings were carried out and supervised in various other chiefdoms at the request of the natives.

Discriminative clearing for the expulsion of tsetse was resumed, large work was done also in the Maswa and Kwimba districts at the request of the Administration; 18,650 tribesmen came out in Buhungukira and an excellent start was made on our five-years scheme in the latter locality.

(e) The year 1934.

In 1934 the isolating barriers of the Huruhuru Plains were lengthened and widened, further water supplies were developed and a general consolidation of the position was carried out. The corridor from the southern chiefdoms was carried further towards the Huruhuru. The important Somageti–Wembere clearing in south-west Shinyanga was made both as a corridor to the eastern part of the Wembere Plain and to break off a large block of country (*see* map 3) from which later to expel the tsetse. Again several clearings were carried out by request in the various chiefdoms.

A further great gain to the tribe was the throwing open to settlement of the " outer circle " in Shinyanga—an advancement into the fly territory of the Chibe salient. Much work was done in other districts as well.

(f) The year 1935.

Work on the main reclamation scheme was continued by the tribe under the direct supervision of the Department. The native administration bore a much greater proportion of the cost than previously.

Further marginal clearings were undertaken to reclaim a further 100 square miles of the Huruhuru Plains. Tanks were added for the storage of a further 5,000,000 gallons of water. The veterinary department seconded an officer to organise the rotational grazing of this type of country reclaimed by us in three districts of the Lake Province. By forming a wet-season outlet for the stock, this will ultimately lead to the scientific grazing of these districts and so remedy the deterioration of pasture that is so widespread to-day.

In Kwimba district the Buhungukira scheme (*see* p. 370 above) has continued with our assistance. The development and exploitation of this area is taking place rapidly.

In Maswa district clearing continued and was now mainly aimed at freeing

from tsetse the great areas cleared in 1934. Two tanks were made also by the Administration.

A considerable programme was completed by us in Kahama and Nzega, to provide land for grazing, to provide land for settlement, to stop a fly advance and to free a cattle-road of tsetse. Continuation of the clearing in Msalala in Mwanza took place.

Three great clearings, chiefly for settlement, were begun in the Central Province under the technical direction and with the help of the Department. Access to the great Masai mbuga was included.

(g) Some of the reclamation schemes.

Details are given in the text on some of the larger undertakings. These may be summarised here as regards the Marialuguru salient, in Maswa district, by saying that our cutting off of this block and the measure—non-burning followed by fierce burning—directed against it, have apparently freed it of flies.

As regards Buhungukira in Kwimba District, the ladder-work of mbugas there was utilised to break the fly bush into islands for future attack, and one large mbuga area, infested but easy to deal with, was cleared to form a grazing area between two lines of hills, on to the feet of which the clearing was carried to provide sites for organised settlement. Water was also provided from tribal funds by the Administration and the Department of Geological Survey, these supplies being furnished by earth-tanks (fig. 25) and a bore-hole.

A piece of country of 150 square miles, divided into four blocks, was selected in Maswa for a further experiment to ascertain the effect of not burning the grass for a number of years, and the experiment was duly initiated.

Some of the above clearings with others not mentioned here have the effect of breaking nearly the whole country shown in map 3 (Lake Province) into blocks, great and small, in which to attack the flies. If the results approach at all the success that we hope for, the resultant reclamation for the benefit of the natives will be great, but it will depend on the continuance of tribal co-operation.

In Nzega was found a case in which *G. morsitans*, advancing, had reached its vegetational limit, but where *G. swynnertoni*, coming in from elsewhere and being able to make use of the vegetation which *G. morsitans* could not use, was taking up the advance. A barrier clearing was made.

Near Mpapwa clearings were made across the valleys of the Tambi and Metamondo streams by the Administration and Veterinary Department, following our recommendations. The object was to stop a seasonal influx of *G. pallidipes* which was increasing yearly and was causing great infection of cattle. The first results of the measure are promising.

The infestation of the Mbulu district and the schemes of reclamation initiated in its northern portion by Tully and developed by Gordon-Russell are described, as is the problem of the Wafiome. On the Ndareda–Babati front both European and native settlement is threatened and each is doing its share towards the formation of a barrier.

The position south of Ufiome Mountain is particularly serious, 9,000 out of a tribe (the Wafiome) totalling 15,000 having emigrated already, partly as the result of tsetse. Our scheme here is the splitting of the narrow belt of *G. morsitans* that runs from Ufiome to Itundwe into blocks by means of clearings. These blocks are then to be attacked by non-burning and by discriminative clearing.

Discriminative clearing in this case will be applied to the main breeding-grounds on the steep scarp north and south of Kikore, the main permanent

home of these flies in this region, and log-traps will be used elsewhere. The barrier cross-clearings (in the lower country) will be settled, and will act also as corridors for cattle to the great open mbuga to the west. The tribal side of the work has already begun both in the Northern and Central Provinces, and our own preparatory experimentation with the traps is well advanced at Kikore.

A scheme has been suggested for the isolation of a strip of country north and south of the Yaida river. It awaits further survey and consideration.

(h) The scheme for opening up the greater mbugas.

There are areas—great plains—that are uninfested but are rendered inaccessible to cattle by bands, broad or narrow, of tsetse bush in between. There are other areas which are infested seasonally only, and others again which are infested continuously not because they are themselves suited to the flies, but because the latter constantly wander into them from real fly bush close alongside.

To reclaim the first type of country it is only necessary to cut a corridor into it through the band of fly bush. To reclaim the other two types it is necessary to make clearings that will isolate them from the fly bush. To find and reclaim such areas is part of our programme.

As an instance in which we have reclaimed an area of the third type successfully, we may mention in the first place the Huruhuru Plains system, which has been broken into by a corridor eleven miles long and cleared of the flies in its wooding by means of a broad isolating clearing running round it. Water supplies have been provided under our supervision, in the form of earth-tanks which each year are being augmented, and 25,000 head of cattle were grazed in the area in 1934, the first year in which it was thrown open. Great numbers more need this grazing and there is room for them.

The summary already given on p. 393 above should be seen for further discussion of this subject. Actually probably 500 square miles will have been reclaimed in this general area by the time the whole work is complete. Fully 150 square miles have by now been reclaimed in the Shinyanga portion alone.

A second instance of successful reclamation is the plain-system of the Manonga, which has been broken into and is used now by thousands of cattle. Thirdly we may mention the Wida mbuga of 50 square miles in Maswa. Corridors have been taken to this from the north and the south, earth-tanks are being made by the Administration, and large numbers of cattle are using the grazing already.

The Ntukuza mbuga in North Maswa, to which it is proposed to carry a short corridor, is typical of many smaller mbugas that are capable of carrying cattle.

The Somageti corridor has been mentioned already. It affords access to the easternmost part of the great Wembere Plain.

The latter plain is enormous and a considerably greater portion of it could be used if further waters were provided, but its broadly wooded margins are being invaded more and more by tsetse fly, and work will probably have to be done for the isolation of a part of these.

The Serengeti of Tanganyika is mentioned solely to discourage the idea of carrying cattle-corridors into these wonderful plains for the introduction of dense masses of Usukuma cattle. These would ruin, as they are ruining their own country, what should otherwise some day be the most celebrated and most visited of all the world's national parks.

A description is given of the work of the Administration and Tribe, which, by cutting through bands of fly bush, is throwing open to the Wambulu the

broad, open expanses of the Kiratu–Oldeani country, which is now called Inchi Mpya, and totals 300 square miles.

The scheme for the opening up of the great north-to-south mbuga that separates Kondoa–Irangi from Masailand, and on which work has already started, has been referred to already.

(i) The settlement of the areas reclaimed.

In parts of the Lake, Western and Central Provinces especially, native settlement is collected into limited pieces of country which it keeps bare of trees and which its cattle keep bare of grass. Alongside are the tsetse areas with their wooding and their magnificent, unused grazing. In the first type of area accelerated erosion inevitably follows the baring of the eluvial ground, and the tsetse fly, therefore, is performing a useful function in holding large areas of good ground in reserve. It would be wrong to reclaim it merely to extend the semi-desert of the cultivation steppe alongside.

At first settlement had to be attracted into the areas we reclaimed. Later no attraction was necessary. Finally it became somewhat of a rush. What was at first the right way became the wrong way, and now, though the reclamation and settlement of new areas is urgently needed, it requires to be carried out under very close regulation of the number of settlers and especially of the number of cattle admitted.

The scheme supported here is that settlement (settlers and cattle) should be admitted on a quota basis, while advantage should be taken of the thinning of settlement anywhere in existing cultivation steppe to apply the quota there also. Cattle, in the reclaimed areas of Shinyanga at least, can be kept at present at an economic level by insisting that the surplus shall be kept on the Huruhuru Plains close by, for seasonally these will support very heavy stocking.

In the meantime every effort should be made to increase the numbers of cattle sold and slaughtered annually, and to make the fullest possible use of the existing cattle as an asset for the upkeep of soil fertility in a proper system of farming. The Department of Agriculture is making an important beginning in the latter direction with its individual native holdings.

In reclaiming land for settlement we have also provided new waters, for without this there is much land that settlement could not enter. Of the four methods used, three have been described under the heading " some reclamation techniques." * The remaining method has been boring carried out by the Department of Geological Survey.

(j) Some reclamation techniques.*

(i) *Technique of clearing.*

Clearings may be made by methods which are either permanent or impermanent. The latter—including mere felling of trees and shrubs—are used where settlement is to be introduced at once on a sufficient scale to keep down re-growth.

In the clearings intended to form the more permanent barriers against the tsetse, all means are employed to prevent re-growth from the stumps. Piling and burning or poison are used and the cost becomes relatively high.

Poisoning and ring-barking share the disadvantage that the trees take a very long time to fall and the clearing remains in the meantime one which the tsetse can pass.

Slicing (described on p. 408) is used for acacias in combination with felling,

* *See* pp. 406–423.

and, for grown trees, is effective. For *Commiphora*, another very abundant tree-genus, it has been found that by ring-barking at ground-level and throwing on a handful of earth, termites are encouraged to attack. They eat out even the roots of a great percentage of these trees and thus produce an excellent clearing.

In poisoning, boring is to be avoided. The poison is dribbled into a frill cut through the bark round the tree. As regards methods for poisoning, and low-strength poisoning, a cheap method of killing trees back temporarily and of delaying regeneration, is regarded as a useful measure in some circumstances.

Tree poisoning cannot be left in the hands of natives, as has been done in some instances, without very grave risk. Antidotes and instruction in their use are a part of our poisoning work.

Experiments in the killing of the roots of stumps to prevent regeneration after felling were conducted in 1935.

The technique of laying out clearings, the " wave " method of attack, the danger of leaving trees standing in clearings that are intended as barriers, supervision, tools, the use of fire in clearings, day work versus task work and the cost both of clearing different bush-types and using different methods are among the subjects discussed fairly fully on pp. 406 to 423.

In 1935 the experimentation for the improvement of the general technique of bush-clearing was continued—experimentation to determine the labour required to clear different types of bush and the most economical way of utilising it.

The experiments which we have carried out in mechanical clearing so far have shown that while thickets and small trees may be smashed down and sawn down by motor traction used in conjunction with rollers and saws, a pneumatic secateur, taking fairly thick stems, is at present the most promising method.

(ii) *Technique of grass-fire control.*

A description is given of this technique and of the special methods developed to meet local conditions. During the four years in question this work has been very successful. Progress has been made in the following salient points. Fire-breaks have been made early in the season, a fire-fighting organisation has been kept ready for use the moment an alarm is given and natives who light illicit fires have been detected and punished in the native courts.

(iii) *Technique of water supply.*

The technique of water supply includes the utilisation of rock-catchment (pl. 16, fig. 2), the making of a coffer-dam (pl. 16, fig. 3) and of an earth-tank (pl. 16, figs. 1 and 4).

(k) Continuity of plan in reclamation work, and the appreciation of the natives.

The original plan of the reclamation work was drawn up in 1923. With the help of the chiefs of the tribe and of the Administration we have developed that plan and worked on it consistently ever since, until it now comprises a scheme for the reclamation of the whole of the blocks, large and small, that fill most of map 3.

The original intention was not confined to the carrying out of reclamation. It was (on the part of Stiebel, McMahon and myself) to encourage the people to attack their own problems and to inculcate a spirit of service. This attempt has been not unsuccessful. The annual happy turn-out of workers in Shinyanga

has become a tribal event and custom and could well continue as such, and much more than the attack on the tsetse would be lost were it to cease.

In 1923 the present Game Warden and I arrived at a residence of Makwaia, the largest Shinyanga Chief. Cotton growing was at that time being urged. Makwaia took us over a clearing which many hundreds of people were making and the cotton from which was to go to themselves. He scattered encouragement and everywhere the tribesmen worked with zest. At the far end we found a contingent that had just arrived. Makwaia made them a speech defining the objects of the work. He ended: " Now you understand why I have called you here; but, if you don't understand, it does not matter. For am I not your father, and would a father tell his children to do that which was not for their good?" The tribesmen received this speech with the greatest enthusiasm.

We saw here an example of the traditional tribal relation between a chief and his people. This spirit has characterised the annual clearings in Shinyanga up till to-day.

FIG. 32.—" The proof of the pudding." Cattle safely grazing Blocks 2, 3, and 5A, in Shinyanga, cleared of *G. swynnertoni* without wholesale clearing of bush. Block 2 (uncleared) seen in background.

The assistance of the Government and the results obtained have been very fully appreciated. On two occasions all the headmen of a chiefdom, with many of their retainers, have come to me with embarrassingly large offerings, particularly of milk. Asked for the reason, their spokesman has replied: " When you started your work here we had been driven out of our land. The few people left could not keep cattle and lived in fear of lions. Now our land is 'peupe' (clear) once more, our people are flocking back, they can keep cattle and no longer fear lions. We have brought these offerings as signs of appreciation and thanks."

In return my staff and I wish to express here their appreciation of the excellent service done by the tribe to the work in which they took part and of the loyal and understanding co-operation accorded to us from the start by the people, their chiefs and the Administrative Officers concerned.

20.—FLY ADVANCES.

(a) The advance in Western Kondoa.

(map 5.)

The advance of *G. morsitans* across western Kondoa into Singida district was studied continuously from 1928 to 1932, and its previous history investigated from British and German records.

It was concluded that an advance of tsetse had taken place from north-east to south-west to a depth of some 50 miles.

The rate of advance was especially rapid in the very wet year 1930, perhaps because this country is very dry and a wet year mitigates its severity. The average rate of advance was about three miles a year.

The more thicketed miombo appeared less favourable to the tsetse advance. Dense deciduous thickets formed barriers which the flies had to outflank. Certain areas of thorn-bush (*Acacia Kirkii*, etc.) formed partial barriers to this species.

The importance of game movements in assisting advance was *nil.*

Road (motor) traffic had absolutely no effect on the advance.

The neighbourhood of large settlements was unfavourable to tsetse.

There was a strong appearance, never finally proved, of a " social " concentration, in the valleys, of the pioneer flies.

Suggestions made for stopping the advance by blocking with artificial barriers the gaps between thickets, could not be adopted owing to the financial depression. The opportunity of stopping the advance on these lines has now passed. The advance has now swallowed the bulk of the country-keeping tribe, the Usandawe. It is continuing, and threatens, after absorbing the small remnant of Usandawe, to enter the north-west Dodoma district.

(b) The Hika advance.

(map 6.)

Since 1927 a " new " belt of *G. morsitans* has become known near Saranda, where the Central Railway climbs the Rift Wall. Since that date this belt has spread out from its apparent point of origin there both southward into the Manyoni district and northward into that of Singida. It is known as the " Hika " belt and its advance appears to be continuing. It was believed by its investigator to owe its beginnings to the flies that are carried on the trains, through the great thicket barrier from the belt of *G. morsitans* 40 miles away to the west.

(c) The advance on Singida from the south-west.

(map 6.)

From the western belt just mentioned a third great advance by *G. morsitans* has taken place in late years, the flies passing through a narrow gap at Matelele, between the great Itigi thicket just referred to on the one hand, and the open grass-land of the Wembere steppe on the other.

The gap was being passed in 1927, when the beginnings of an attempt were made to block it while the advance still could have been stopped. The work was unfortunately not continued in subsequent years, and the advance has progressed towards Singida and Mkalama, on an ever-broadening front, at the rate of four miles a year.

(d) The advance on Singida from the north-east.

(map 6).

A belt of *G. swynnertoni*, originating somewhere north-east of Mkalama near Lake Eyasi, has advanced southward and westward, between the Mkalama cultivation steppe and the open plains about Hanang Mountain, the country of the Barabaig cattle-keeping tribe.

This advance has now arrived near the northern border of Singida district and threatens that district also. The speed of this advance has been, lately, about one mile a year, but acceleration is now reported.

The advance has now reached a point where it must pass through a bottle-neck, 11 miles in width, between the open cultivation steppes of Singida and Mkalama.

(e) The position in Singida generally.

(maps 5 and 6).

There are thus four advances, three of *G. morsitans* and one of *G. swynnertoni*, converging upon Singida from all four points of the compass.

An inter-departmental conference was held at Singida in 1934. This conference supported the scheme of locating the concentrated settlements, that were to be called into existence by Dr. Maclean to forestall the threat of sleeping sickness from Mkalama, in such a way that they would form barriers across the fly advances.

Clearing was thus begun in 1934 to safeguard the remnant still uninfested in Singida (about a quarter of the district) and to check the advance of the western belt of *G. morsitans* towards Mkalama, by connecting the Singida cultivation steppe, by means of a two-mile-wide clearing, to the Wembere steppe, advantage being taken of some areas already under settlement. The work is continuing, and is in the nature of a race with the tsetse.

A survey by Burtt in 1935 showed, on the Rift Valley side, that the flies were already across the clearing, and had ascended the scarp. He arranged for a new clearing to be made in front of the flies that had crossed. It was hoped that these measures, together with settlement and destruction of a herd of buffalo that crossed back and forth at this point, would save this part of the line, but this hope seems unlikely to be fulfilled.

(f) The advance on Lakes Basodesh and Basotu.

The above-mentioned belt of *G. swynnertoni* threatens also the Barabaig country, but its advance eastward has become slow in recent years. About 300 square miles have been abandoned by the tribe already.

Clearing has been done here already by the Administration, but further careful survey is now needed with a view to the choice of a method of attack on this fly belt.

(g) The advance eastward and southward in the south Masai steppe.

(map 1.)

The southern Masai steppe and, ultimately, the country round Dodoma, all shown light blue on map 1, are regarded as threatened by advances of fly from the area shown dark blue on the map in their north-west, though the advance that was taking place here appears to have slowed up of late (p. 438).

The general position as regards the fly advances is summarised on p. 438, Section H.

21.—CO-OPERATION WITH OTHER TERRITORIES AND WITH OTHER DEPARTMENTS.

(a) General.

Friendly co-operation has been established with Kenya and Uganda, and correspondence with other countries and territories.

In Tanganyika, we have worked in harmonious co-operation with the Medical, Veterinary and other Departments, to the work of which ours is complementary.

(b) Co-operation with Kenya Colony against *G. palpalis*.

A joint experiment with Kenya in the use of traps against *G. palpalis* is in progress on an island near Kisumu. This experiment was started in October 1932. The density of the flies in November 1933 was less than half that observed in November 1932 and during April 1935, as deduced from the fly rounds, it was less than half that of April 1934, the month chosen in each year being the month of greatest density. The tsetses have been much reduced, but very far from exterminated. The best trapping season is from January to May, and the largest catch was 26,160 flies in February 1933. Further experimental measures are planned for the extermination of the flies on the island.

Advice has been given to the Medical Department, Kenya, on a scheme for freeing the Kuja river, in Kenya, from *G. palpalis*, which carries human sleeping sickness. The riverine wooding is being split into sections by the clearing of fords, and each section is attacked by means of traps till density is reduced to the point beyond which the traps make no impression. The attack is then continued by means of hand-catching. It was hoped that these measures, starting from the tributaries and continuing downwards, would if successful follow the main rivers and, on reaching the Lake, be extended along the shore. In this way it might even be possible to achieve a complete solution of the problem of *G. palpalis* in east Africa.

The site of the operations has been revisited more than once, and R. T. Vane, previously of our Department, is in charge under the Medical Entomologist, Kenya, C. B. Symes.

Already the results reported are " the freedom from *G. palpalis* of the upper portions of the Nthiwa and Pala streams and the reduction of the fly to a low density on about a mile of the Kuja river. From five to six square miles have been made available for settlement and settlers are establishing themselves. . . . The method appears to be practical and economical. It is to be continued with local funds for the progressive elimination of *G. palpalis* down the Kuja river." *

(c) Co-operation with, and visits to, other territories north of Tanganyika, in relation to *G. pallidipes* and *G. morsitans*.

Advice has been given on a not dissimilar scheme for the study and removal of *G. pallidipes* in the Lambwe valley in Kenya. Here again Commander Blunt has been transferred from our Department to take charge of the work under the Veterinary Entomologist, Kenya, E. A. Lewis.

Clearing across the valley has been carried out in order to form an island of fly-infested country for experimental attack, and as the beginning of an attempt to ascertain the distances to which *G. pallidipes* will traverse a cleared barrier locally. Breeding habits are being investigated, and also the relation

* C. B. Symes, Report of September, 1935.

to elephant and buffalo. Traps are being tried and improved, discriminative clearing is to be applied to the local conditions and other observations are in hand.

Visits of advice were paid to the Kenya coastal strip.

One of our own entomologists, Moggridge, has been stationed at Kilifi on the Kenya coast for intensive research on *G. pallidipes* and *G. austeni*, which will include, ultimately, the study of these flies in every sort of environment. The work at Kilifi started in the last months of 1935.

In 1935 Moggridge spent a month in Italian Somaliland investigating *G. pallidipes*, *G. brevipalpis* and *G. austeni* in the Juba river area and *G. pallidipes* in that of the Webbe Shibeli. The main conclusions, other than those relating to distribution, drew attention as regards *G. pallidipes* to its close concentration in limited areas in the dry season—pointing to the possibility of control; to its spread to a depth of six miles in the rains, and to the need of relatively high humidity in the area invaded; to its invasion at this time of a great, intensively cultivated area, following the scrub growing along the main irrigation channels, far apart and using banana plantations; and to its carriage by natives bearing loads, these being apparently the attraction.

Another of our entomologists (Jackson) visited Uganda in 1932, advising on details of work in progress or contemplated, and demonstrating technique in the field. Other visits have been paid to Uganda—to the trapping experiments against *G. palpalis* on Nadzi Island and the large-scale reclamation work against *G. morsitans* being carried out in Ankole by the Veterinary Department.

(d) Visits to Northern and Southern Rhodesia, the Union of South Africa, and Nyasaland.

R. W. Jack, Chief Entomologist, Southern Rhodesia, has been kind enough, on three occasions, at intervals of a few years, to show me over parts of the area of his work in arresting a *G. morsitans* advance by the erection of game-proof barriers and the destruction of the game animals between. The last occasion was in 1935, when the retreat of the flies was confirmed in the region of the Nyamparni Vlei, seen by me, and the barrier against *G. pallidipes* on the Melsetter border visited.

I am much indebted to R. H. T. P. Harris, Director of Tsetse Control Operation, Zululand, for allowing me to see the work in the Umfolozi Reserve in Zululand in which *G. pallidipes* is being attacked by means of large numbers of Harris traps. This seems likely at least to succeed in reducing the flies so far that invasions from the fly belt proper on to the farms and native reserves surrounding it will be negligible.

I am also indebted to Colonel Stevenson-Hamilton for taking me over a portion of the Kruger National Park, a visit which suggested ideas on the effect of the Great Rinderpest in relation to the extinction of *G. morsitans* in this area.

Dr. Lamborn in 1935 showed me his interesting and successful resistance to an advance by *G. morsitans*.

On the invitation of the Northern Rhodesian Government, I visited the Abercorn district late in 1935 and, after studying the threat by *G. morsitans* to native reserves, the farms held by Europeans and the land of the British South Africa Company, advised certain measures. It is believed that control (in this case, of *G. morsitans*) is possible. Measures recommended for the farming area were the injection in every case of sick animals, the picketing of certain paths, an attack on two fly concentrations, by native settlement especially, and—as a general measure, which would be useful to the planters, the native reserves and the land in the hands of the British South Africa Company—the prevention of grass burning. A wet-season investigation was recommended.

The district is also well suited to a watched and controlled experiment in the early burning of grass, which I should very much like to undertake, as part of our experimental programme.

22.—OTHER MATTERS OF INTEREST.

Numerous papers have been published and lectures given by members of the Department during the period under review.

In 1934 a museum was started in Shinyanga for the benefit of visitors and ourselves. It illustrates the ecology of the tsetse flies and the scope and history of the work.

A small zoo has been started in connection with our studies on the blood-foods preferred by tsetse flies.

A Masai belief that locusts drive out tsetse is referred to. Our observations so far contradict the belief.

The experiment in keeping cattle in areas infested by fly is mentioned. Cattle can be maintained thus by means of fortnightly injections of Tartar Emetic. No resistance is developed, for if treatment is discontinued all eventually die.

A discussion is included (p. 464) of the inter-relations of the tsetse and man.

23.—PROSPECTS AND NEEDS OF THE WORK.

(a) Prospects.

It is felt that, while trapping or other methods of direct attack will be useful in localised areas, only the alteration of the environment generally, or of some one item of it that is essential at one time of year, will be successful on a great scale.

We are confident that, after further field experiments in this connection, we can add very greatly to the areas we have reclaimed already in Tanganyika.

(b) General needs.

To conduct this investigation, however, and to procure this success, we need further staff and money. The items of extended programme for which these are required have been stated briefly on pp. 469–472.

In Shinyanga our experiments against *G. swynnertoni* are greatly hampered by lack of funds to isolate adequately, *e.g.* our separate experimental blocks.

Again, though we have studied *G. morsitans* very fully we have not had the money for putting our conclusions to the test of experiment. Now plans have been made and some of the sites for large-scale experimental work have been chosen. If the necessary funds can be obtained it is hoped very shortly to begin work against this fly on the field scale employed heretofore against *G. swynnertoni*.

Other species of tsetse are also to receive attention if funds are available. *G. pallidipes* especially is a species of the very first importance; for, overlapping *G. morsitans* and *G. swynnertoni*, it may seriously affect the success of our work against both these species unless we know how to deal with it. *G. palpalis*, *G. austeni* and *G. brevipalpis* will also receive attention. *G. austeni* may prove very important.

A good laboratory is lacking and is very much needed.

The game experiments should be continued as planned, and our very thorough study of the relations of the several tsetses to their several food animals, developed and prosecuted. It is essential also to find some practicable method of arresting a fly advance.

Advice to other Territories will, moreover, be needed.

All the requirements set out above will demand for their fulfilment both staff and money.

(c) Policy.

It is essential that when tsetse measures or important experiments are initiated, appropriate steps should be taken by the Administration to ensure that District Officers should collaborate in every possible way with the Tsetse Research Department, in order to bring the investigation to a successful conclusion. Such steps are particularly necessary on the first appointment of District Officers to districts in which investigations are in progress.

(d) Organisation.

As a result of our experience in Tanganyika and of that of workers in other Territories, I am convinced that in heavily infested Territories tsetse investigation and control can only be effectively conducted if it is entrusted to a separate and permanent organisation independent of existing Departments of Government. It is only in this way that a broad and considered policy can be formulated for dealing with the manifold problems involved and the necessary continuity secured.

PART 13.—CONCLUDING NOTE.

The present paper serves to show that a great amount of varied investigation has been attempted on every aspect of the problem, and that, thanks to the devotion, energy, team-spirit, and efficiency of the staff, a great deal has also been accomplished. An excellent beginning has been made with the study of the ecology—the reactions to their environment—of the flies, in order to discover the weak points in their defence and to deprive them of one or other of their vital requirements. Several species have been so studied and promising lines of attack against certain of them are in course of development; and a study of the food animals of the flies on the same lines has been begun. At the same time all possible steps have been taken to apply practical measures of control, an elaborate programme of survey and reclamation having been carried out by methods the efficacy of which we have already established. The work of Lamborn in Nyasaland, Jack in Southern Rhodesia, Harris in Zululand, Symes on the Kuja in Kenya and by Buxton and Nash (a former member of our staff) in Nigeria has produced results which have added still further to the progress achieved in the period under review.

The results which we have obtained are already proving valuable in the attack on the flies. Solutions are being obtained for particular tsetses under particular conditions, *e.g.* for *G. palpalis* (p. 508 above). Much country has been reclaimed for Tanganyika, while the work already planned or begun holds out the prospect of still greater success in the future. It should be realised that however effective may be the methods of control evolved by our research, an expert entomological organisation will always be necessary to plan and direct the application of those methods. These methods should form part of a general scheme of development which, once adopted, should be adhered to, so far as possible, without sudden change. An expert organisation of the kind suggested will always be required to adjust those methods to meet the varying problems created by the existence of numerous species of tsetse, and by the fact that each variation in the natural environment of any species may demand a different combination of measures.

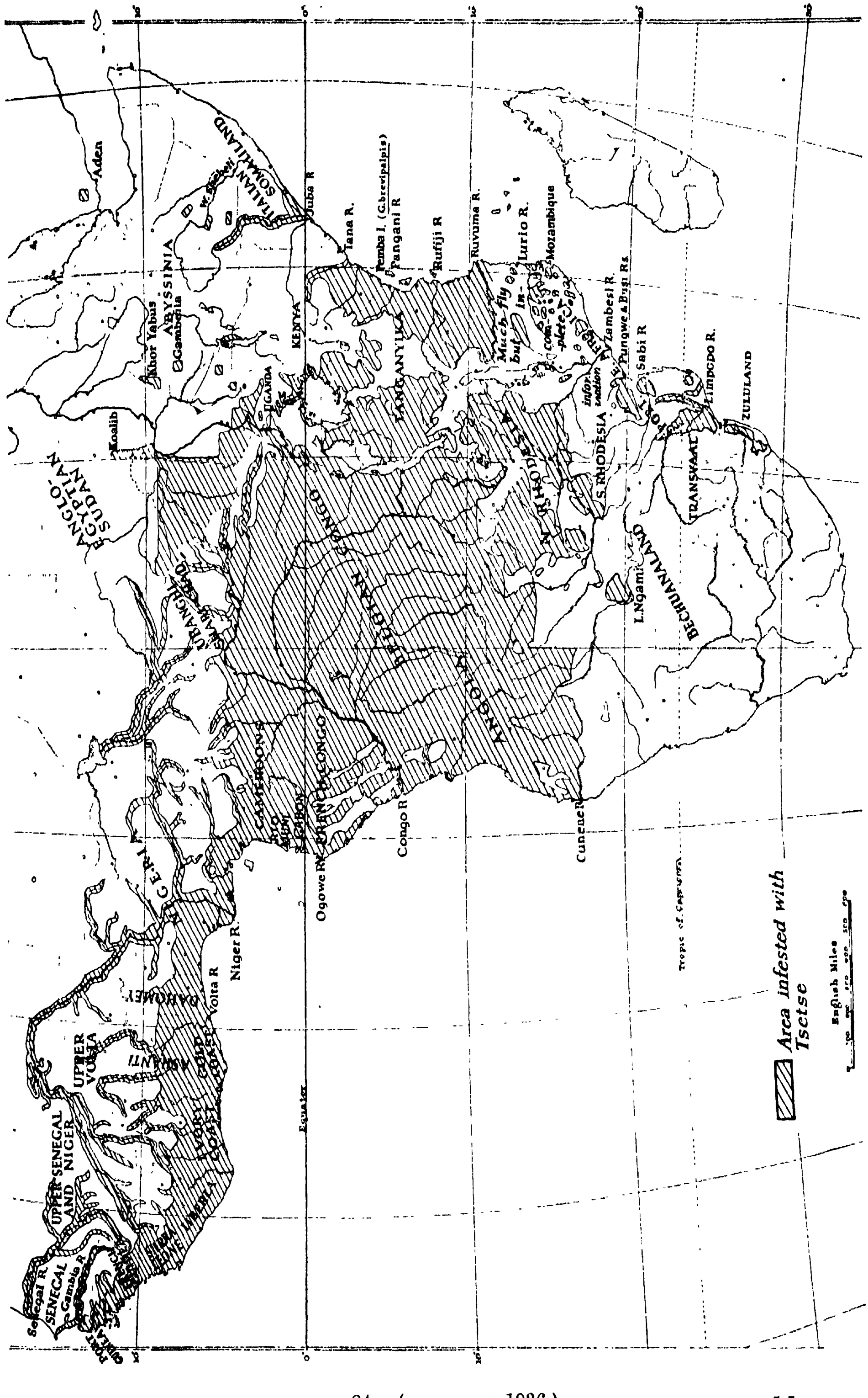

FIG. 33.—The distribution of the tsetse flies in Africa.

APPENDIX 1.

DEFINITIONS OF CERTAIN OF THE TERMS USED IN THE PRESENT PAPER.*

Activity.—The disposition of the tsetses to show themselves to the catchers and to be caught.

Aerial factors.—The above-ground physical factors of the environmental complex, *e.g.* solar radiation, air temperatures and humidity, sunshine, light intensity, and wind.

Anti-countershading.—That type of coloration in animals in which conspicuousness is attained by the upper parts of the body being white or pale and the lower parts dark as in the skunk. It accompanies highly nauseous qualities.

Assembly or assemblage.—These terms are used in the present paper for the animals as a whole that are found in a plant community. The distribution of animal species continually cuts across that of the plant communities. Moreover, as the result of (*a*) mobility, enabling food and water anywhere to be reached, and (*b*) the use of different plant communities for different purposes, there is far greater variation and fluctuation in the animal element in an ecosystem (*q.v.*) than there is in that of its plants. It is for this reason and in order to emphasize this difference, that I have used the present word with (*a*) its implication that there need be no permanent connection, and (*b*) its suggestion of importance making it applicable to the greatest of animal aggregations. The assembly may, however, include a true community or communities which are definitely attached to and characteristic of a particular plant community or of an ecosystem. Thus, the water-margin assembly contains also a zonation of communities; while rain forest shelters a highly characteristic animal community, although savanna birds which use the openings in it and the tops of the trees, and elephants and buffalo which use nearly all types of country must also be included in its general "assembly." This existence of communities proper is stressed on p. 54.

Association.—A major community of plants consisting of a definite assemblage of species with a definite habitat and dominated by two or more species, such as the oak-beech forest of Europe. The term is applied normally to the final "climatic" climax (*see* "climax, vegetational"), stages characterised thus on the way to the climax being denominated "associes." Our major east African communities, being each in effect a climax, though in places non-burning may change them, are here conveniently termed "associations."

Atmometer, Livingston.—A type of evaporimeter for estimating the evaporative power of the air. *See* "evaporation-rate."

Bait-cattle.—Cattle used for making tsetses appear, when unwilling to show themselves to man, the cattle being preferred.

Barrier ("fly" or game).—A natural or artificially made barrier or fence which tsetse or ungulate mammals cannot pass, or (in the case of the flies) cannot pass in sufficient numbers to form a colony beyond it.

* The present paper has been written not for scientists only, but for the general public also.

Biome.—" The whole complex of organisms, plant and material, present in an ecological unit " (Tansley, 1935).

Biotic factors.—The living components of the environment, though frequently in the use of the term the action of animals is visualised—as grazing by cattle or burning of grass by man.

Blood-predator.—Suggested as a term for an animal species which " preys " only on the blood of other animals. It does not maintain a continuous contact with them, as does a parasite, but must find each meal by a fresh search. Examples are tsetse flies and vampires.

Blood-prey.—The supplier of blood to the blood-predator.

Buffer.—A species which, preferred or more available, diverts, largely or temporarily, the attention of predators from another species of prey (table 40).

Case, or Shell.—*See* " puparium."

" Cement."—A concrete-like hard-pan, in this case limey or marley, below the soil surface (*see* p. 86).

Chain of attack.—A series of species of animals and plants associated as attackers and attacked and regarded in the sequence in which each member of the series feeds on or destroys one or more of the other members (*see* table 40).

Characteristic species.—A species, not necessarily dominant, that characterises typically an ecological unit. *See* " dominant."

Chemotropism.—Attraction to the source of, or (*e.g.* in mammals and birds) decision to accept or reject prey in response to, a chemical (olfactory or gustatory) stimulus.

Climax (vegetational).—" A relatively stable phase reached by successional change in the vegetation " (Tansley, 1935). The term " climatic climax " is applied to " the highest vegetational types under the prevailing climates " that are limited only by climate. " Other climaxes may be determined by other factors such as certain soil types, grazing animals, and the like."

Coffer-dam.—An artificial barrier of masonry or clay across a sand river, and built on a clay or rock bed, to prevent the water in the sand from seeping away down-stream (pl. 16, fig. 3).

Colluvium, colluvial.—A soil deposit in process of being carried by water, wind, or other physical action from eluvial rise down to alluvial plain.

Colouring, protective, procryptic, secant, warning.—*See* "procryptic," "secant," " warning."

Community.—An aggregation, large or small, of animal and/or plant species naturally and usually living in company with each other. This term is used in a different sense to that applied to " assembly " (*q.v.*).

Concentration, tsetse.—A permanent, seasonal or more temporary aggregation of tsetse within a small area, which supplies every need of the flies during the period of the aggregation, and which is surrounded by country in which they are scarce.

Concurrence of requirements.—The concurrence in a sufficiently limited area of all the vegetational types which a species, tsetse or other, needs for its feeding, resting, breeding, and other requirements. *See* " edge-effect."

Consociation.—A community (within an association) dominated by one only of the dominant species of the association. As a wood dominated by *Brachystegia* within the general *Isoberlinia-Brachystegia* association. Part of a vegetational climax, such a community in a developmental stage being termed a " consocies." *See also* " association."

Countershading.—The type of coloration of animals in which the upper parts are darker and the lower parts lighter. Regarded as (*a*) concealing, (*b*) indicating that the under parts are commonly concealed or otherwise unimportant to the colour scheme.

Cultivation steppe.—An open area under sufficiently close human occupation, agricultural, or agricultural and pastoral, to have been cleared of the greater proportion of the natural woody vegetation (pl. 18, fig. 2).

Dambo.—*See* "mbuga" and "vlei."

Densification potential (D.P.).—The latent ability of a given vegetational type or area to develop into thicket or denser woodland on the exclusion of the annual grass fires. Examples in pls. 11 and 12.

Density-activity.—The true density (*q.v.*) of the population, the disposition of the flies to show themselves to the catchers, and the ease with which they can be captured when seen. Measured in combination by the mean number of tsetse caught per unit distance or unit time.

Density, lowest.*—The population of a species over a given area including blocks in which the species does not occur.

Density, economic.*—The density in which a species occurs in its actual habitats.

Density, highest.*—The density in which a species occurs in its concentration-sites.

Density, true.—The number of tsetses (or other animals), visible and invisible to the catcher, or observer, present in a unit area. For the method of ascertaining this *see* p. 36 and appendix 3.

Directive or "traitor" species.—Species the presence of which, instead of acting as a buffer (*q.v.*), will tend to draw predators to a site in which they will also find a species of prey that otherwise might have escaped. *See* table 40.

Discriminative clearing.—*Either* the complete removal of the vegetation from only the sites that are essential to a species of tsetse or other animal for the fulfilment of one of its requirements at one time of the year, or the mere removal of certain vegetational elements from such favoured sites or from the country as a whole.

Distance allowance.—The width of the strip on each side of a transect or traverse within which animals are seen, or (birds) heard, and so recorded as to their numbers, *or* the mean distance on each side of the transect from which biting flies are attracted to the catchers.

Dominant.—The most abundant of the controlling species of a plant community (*e.g.* of the *trees* in a wood), and the most abundant species in an animal assembly. A dominant species must be distinguished from a characteristic species. Thus sable antelope is a characteristic species of the miombo, but it is far surpassed there in numbers by species that occur equally elsewhere, as eland. *Co-dominant.*—One of the two or more outstandingly numerous species in a community.

Drift experiment ("Catching-out experiment").—An experiment involving in the present connection the continuous catching and recording of the tsetses, as they arrive, by a stationary party of catchers over (usually) several hours, during which (usually also) meteorological instruments are read at short intervals.

Dry thorn-bush.—*See* "nyika" and pp. 85–89.

Duricrust.—Used for a greyish-yellow, cement-like soil overlying the original

* After Elton, 1933: 51–52.

granite peneplane of much of the Central Province in Tanganyika in the Rift Valley region, clothed with a unique type of deciduous thicket (pl. 17).

Ecidio-climate.—The eco-climate of a very small place, from Οἰκίδιον, "a little house." It is proposed on p. 45 in substitution for micro-climate, as applied to the climates of nooks, grooves, leaf-surfaces and other small places. The unsuitability of the word micro-climate has been pointed out by Sir Napier Shaw (1929 : 217) (*see* Kirkpatrick, 1935 : 9 at bottom), but a word is definitely required which, for example, distinguishes the eco-climate of rot-holes and grooves in the bark or under a lying log, used by the tsetse for breeding or lying up, from the more general eco-climates of the savanna wood or thicket in which these occur.

Eco-climate.—The climate of the home of a plant, or animal, from Οἶκος, a house or home. The climate of the actual medium in which an animal lives (Uvarov, 1931) as contrasted with the standard climate in the open of the usual ecological station. Thus the climates under rain-forest canopy are those of the home of great numbers of species of birds and insects and are eco-climates. So is the climate of the holes in the ground in which rabbits or wart-hogs may shelter and the hole made by itself in an acacia which a longicorn larva may inhabit (*see* Uvarov (1931), and Kirkpatrick (1935)), but for these a subsidiary term is proposed above.

Ecology.—The study of plants and animals in relation to each other and their whole natural environment.

Ecosystem.—" The biome considered together with all the effective inorganic factors of its environment . . . the organisms and the inorganic factors alike are *components* which are in relatively stable equilibrium " (Tansley, 1935).

Ecotone.—A transitional strip separating two plant communities. In east Africa the intervening strip is not usually transitional in the sense of containing a mixture of the plants of the two communities but has its own separate character and is therefore called by us not ecotone but interzone.

Edge-effect (Leopold, 1933).—The favourable effect on animal population density of the concurrence or interspersion of the two or more vegetational types which between them supply all the different needs of the animal species concerned. *See* " concurrence of requirements " and pls. 3 and 13.

Effective strip (Leopold).—*See* " distance allowance."

Eluvium.—A soil produced on the spot by decay of the country rock underlying it.

Emergence-rate.—The number of tsetse added by emergence from puparia to unit adult population in unit time.

Environmental complex.—The combination of biotic (living) and physical (non-living) factors together constituting the environment in which a plant or animal is living. *See* " ecosystem."

Epigamic.—For the purpose of pairing. *See* " queue."

Evaporation-rate.—The evaporative or desiccatory power of the air, expressed as cubic centimetres of water lost from an atmometer (*q.v.*) in unit time.

Factor.—A constituent of the environment. For biotic and physical factors, etc., *see* separate entries.

Feeding-ground, feeding-haunt.—That part of the habitat to which tsetse flies repair under the stimulus of hunger. Usually an area of higher visibility and higher light-intensity, and exposure (pl. 3 and pl. 13).

Female percentage, old.—The old female percentage is the percentage of females in a sample from which young flies have been excluded.

Ferruginous crust.—*See* " limonite."

Fire-climax.—*See* " sub-climax."

Flights, assembling.—*See* " following swarm."

Fly beach.—A sandy or pebbly beach on the shore of Lake Victoria, usually covered when the lake level is high, and at other times, if shrub-cover be present, used as a favoured breeding-ground of *Glossina palpalis*. Old beaches lie back from flood level.

Fly belt.—Any area of country or " range " throughout which tsetse of any particular species is encountered, however sparsely, in the whole year or a part of it. The varying sizes of fly " belts " or " ranges " may be seen in map 1.

Fly-per-boy-hour (F.B.H.).—The number of flies that can be collected by one catcher (usually one of a pair) in one hour. Used sometimes for stationary and sometimes for progressively moving catches.

Fly-per-boy-100-yards (or 10,000 yards).—The mean number of flies that can be collected by a person per 100 (or 10,000) yards of transect.

Fly-per-screen-100-yards (or other distance).—The mean number of flies that can be collected off a bait-screen (pl. 10, fig. 2) by its two carriers per 100 yards (or more) of transect.

Fly round.—*See* " round."

Focus.—The site of an aggregation of tsetse. A *primary focus* is a site that continues through all seasons to support such an aggregation, and from which impermanent *secondary* foci are seasonally supplied with flies.

Following swarm.—A crowd of non-hungry male tsetses accompanying an animal or a vehicle, and believed to be awaiting the arrival of female flies.

Food-chain.—*See* Chain of attack. The latter term, now proposed, is preferred in order to bring into the picture animals such as man (who is very important) and the beaver which destroy for other purposes than food.

Formation (of plants).—" The plant formation is the major unit of vegetation. . . . Each plant formation is a product of the climate and is controlled and delimited by climate." Each may include several associations. The term " formation " is a synonym of the term " climatic climax " (*see* " climax (vegetational) ") (Clements, 1929; 1936). I have, however, used it here for the whole miombo, including not only the miombo association but also for the acacia and other associations that occur as strips or enclaves in it or under the same climate border it, and for the general dry thorn-bush, including local enclaves of miombo, *Combretum*, etc.

Fossil mbuga.—Mbuga (*q.v.*) that has long become drained through erosion, either intersecting it or leaving it high and dry as on a hill-top.

Fringing forest.—A fringe of forest, usually but not always dense, following streams perennial, seasonal or diverted, to a width of from a few to one hundred yards or more and living on the subsoil moisture. Many types exist, from rain forest to deciduous thicket. *See* fig. 16, also pl. 3, fig. 2, pl. 4 and pl. 14, fig. 1.

Furniture.—Suggested here for the *objects* in the home of an animal which for one purpose or other it needs or insists on having. Such objects are the lianas, logs, rot-holes and rocks under which tsetse females larviposit and rest; the yellow leaves chosen by some yellow butterflies for their resting-places (*e.g.* yellow female *Catopsilia florella*) and the dry leaves or lichen thus selected by insects resembling dry leaves or lichen; the habitual nesting-places of a species of bird or the types of perch it selects for song or (drongo and roller) as a hunting base or (parrots) to rest on.

Gall-acacias (German, *Flotenakazien*).—Trees of the genus *Acacia* which are characterised by more or less globular galls, set between the pairs of straight thorns, and inhabited by ants of the genus *Cremastogaster*. These trees grow mostly on heavy alluvial soils, often in extensive communities from which other tree species are nearly absent. Several species exist. Young trees of *A. formicarum* are shown in fig. 31 and the appearance of gall-acacias in air photographs is shown in pl. 3, fig. 2, in the square space in left-hand top corner (vertical, at 5000 feet above ground), and in pl. 12, fig. 3 (extensive pale wood in mid distance; oblique).

Gallery-forest.—*See* " fringing forest."

gambiense.—*Trypanosoma gambiense* Dutton, the protozoal causative agent of human sleeping sickness in west and central Africa, carried, in nature, by the tsetses *Glossina palpalis* and *G. tachinoides*.

Game round.—*See* " round."

Grid.—A regular system of paths or lines laid out for repeated study of the plants or animals found along them, as in fig. 7.

Home (" true habitat " of Nash).—That portion of the tsetse-habitat used by the tsetse, especially *Glossina morsitans*, for both resting and breeding.

Hotel.—That portion of the tsetse habitat which can provide facilities to the tsetse for *every* purpose—resting, breeding, and feeding. Especially of " hard-pan " vegetation in relation to *Glossina swynnertoni* (light-coloured areas in the wooding in pl. 13, fig. 1).

Hunger cycle.—The mean period elapsing between the tsetse's meals of blood. Sometimes used also, in a theoretical sense, as the time taken for an initially gorged fly to reach a given state of hunger.

Hunger ratio.—A superseded expression, replaced by Mean Hunger Stage.

Hunger-stage.—One of the four groups to which mature male tsetse flies are conventionally assigned on the basis of their state of hunger. These stages are determined by external examination in the field. *See* pl. 21.

Hunger-staging.—The technique of assigning tsetse flies collected in the field to the several stages of hunger (pl. 21 and pp. 37–40).

Hygrometer, paper.—A piece of paper used to measure atmospheric humidity by determination of the weight of water taken up by the paper (*see* p. 45).

Hygrometer, whirl.—Wet- and dry-bulb thermometers set in a frame which can be whirled on a handle, used for the accurate determination of air temperature and humidity at the moment.

Indicator.—Here used for a plant or animal, or plant or animal community, the presence of which can be used as a measure of the conditions.

Interspersal, vegetational.—*See* " concurrence of requirements."

Interzone.—Proposed by Jackson to signify a narrow or wide vegetational strip, separating two larger communities, and including tree species absent from either of them. Opposed to ecotone (*q.v.*), which implies a transitional mixture.

Intolerance.—Used herein for the irritability of certain animals—their unwillingness to be fed upon by tsetse as evinced by stamping, switching, departure or (monkeys) catching the flies.

Key site.—A site the modification or elimination of which alone will drive the tsetse from a far greater extent of country.

Lag.—The delay between the action of a causative factor and the response produced.

Larviposition, rate of.—The number of tsetse larvae deposited per unit population of adult tsetse in unit time.

Limonite (syn. Ferruginous crust and Marram).—Iron-oxide concretions commonly forming a crust below the surface of the ground; for some of the exposed rock, *see* fig. 6. Commonly called laterite, but in most cases not laterite.

Lincoln index.—*See* "recovery index" and appendix 3.

Loitering (as in "loitering ground," "loitering males").—Referring to the practice of the male tsetses of awaiting in suitable situations the arrival or passing of the females.

Management.—Action intended to produce the combination of conditions that will make a piece of country a completely suitable habitat for a species of animal or plant—such as might be applied in a game sanctuary. Conversely the act of modifying existing conditions in a piece of country to the point of rendering it unsuitable to a pest animal or plant—as bush-pig or tsetse, or the thicket in which both lie up. Pl. 11 and pl. 14, fig. 2, represent the effects of "management," the former in favour of bush-pig or kudu, the latter in favour of the plains game, but both to the disadvantage of the tsetse. For a more specialised and limited use of the word *see* Leopold 1933 : 452.

Massive wooding.—*See* fig. 13.—"Large trees in masses or very heavy masses of shrubbery" (Fiske, 1920).

Mbuga (Kiswahili).—Broadly, any open plain. Mostly used to signify more or less open grass-covered alluvium, seasonally swampy. Pl. 3, glade B in fig. 1, open area B in fig. 2; pl. 4, foreground, pl. 13, fig. 2, pl. 12, fig. 3. *See* SSG (seasonally-swampy grass-lands) of map 7.

Mean Hunger Stage (M.H.S.).—The mean or average stage of hunger of a sample of flies composed of individuals which may be in various stages (pl. 21).

Miombo (Kiswahili).—Wooding of *Isoberlinia-Brachystegia*-other genera, described on pp. 48–49, 59 and 81–82, and shown in fig. 8 and pl. 11.

Model, in mimicry.—The insect, bird or other animal the nauseous or other unpleasant or refractory qualities of which render it a subject for protective "mimicry" by less well-protected animals.

Mulch.—The matted remains of last year's unburned grass.

Nagana.—Trypanosome disease of stock.

Nauseous.—Unpalatable to predators or deleterious to these when eaten.

Nook-climate.—*See* "eco-climate."

Nyika or dry thorn-bush.—A type of savanna woodland described on pp. 85–90, and shown in pl. 1, pl. 3, fig. 1, pl. 5, figs. 1 and 2, pls. 12, 13, 14, 15, pl. 18, fig. 1, pl. 20, fig. 1; text-figs. 3, 6, 26, 32.

Old flies, mature flies.—Tsetse which have had their first meal, with the effect of hardening their chitin.

Parasite.—Used sometimes herein for certain parasitoids, insects which, free-living in the adult state, lay eggs, from which parasitic larvae hatch, in the pupae of the tsetse. Hyper-parasite is used for those which thus parasitise a "parasite."

Phenological observations.—Observations on the state of the vegetation through the year—date of flushing, yellowing and fall of leaf, drying of grass, etc. Applicable to animals also—as dates of emergence of broods, of calving or of migration.

Physical factors.—The non-living constituents of the environmental complex, such as soil and climate.

Piling.—Building a pile of fire-wood round the base of a tree or stump with a view to killing it by subsequent burning. The correct method is shown in fig. 27, 5.

Pioneer species.—The first species colonising an area, whether after devastation or on change of conditions. Applicable both to plants and animals. Example the young *Teclea* trees shown in fig. 18.

Precipitin test.—The specific diagnosis of blood sera by a delicate protein reaction known as precipitation.

Predator.—An animal which kills another—or destroys its eggs—by attack from outside. Predators are divisible into classes as suggested in table 40.

Preference experiments.—Investigations into the relative acceptability of different foods to any species of animal.

Primary survey.—To be distinguished from reconnaissance, " aims at a complete systematic record " of the distribution of the chief vegetational types (association and consociation at least) over an area (Tansley and Chipp, 1926 : 42). *See* map 4.

Procryptic or protective coloration.—The colouring of an animal that resembles its normal background, or a background which it selects when the need for concealment arises, or some particular inanimate object whch the animal is protected by resembling. In each case suitable habits must accompany the colour resemblance, the combination being regarded as an effect of natural selection.

Puparium.—The shell or case, actually the last larval skin, in which the tsetse pupa is enclosed. These puparia can be recovered from dry sites up to several years after deposition.

Pyramid of numbers.—A pyramidal arrangement of prey and predator to show that " the number of individuals gets smaller as each stage in a food-chain is reached." This " does not, of course, apply to food-chains of parasites which get smaller and smaller with individuals more numerous at each stage " (Elton 1933 : 30).

Pyrophobe.—A tree, shrub or herb not adapted to survive the annual grass fires (Swynnerton, 1917). *See* fig. 8.

Pyrophyte.—A species of tree, shrub or herb so adapted (*id.*) as a rain-forest tree.

Quadrat.—" A square area, temporarily or permanently marked off as a sample of any vegetation it is desired to study closely " (Tansley and Chipp, 1926 : 58). It may vary in size from a square metre to an area of many square miles for the study of forest vegetation.

Queue, epigamic.—A line of male tsetses scattered along a path awaiting the arrival of a female. Especially common in *G. brevipalpis.*

Radius, cruising.—The distance between the occurrences of an individual animal at different times of the day or year or as between different years (Leopold, 1934 : 450). *See* fig. 7 for the movements of a single month.

Rain forest, tropical and temperate.—Closed evergreen forest growing in areas of considerable rainfall. Fig. 16, also pl. 6, extreme left and elsewhere. At an elevation upwards which varies with the latitude tropical rain forest gives place gradually to temperate rain forest of similar general appearance but characterised largely by other species and a less abundance of lianas.

Reconnaissance.—A type of tsetse, botanical and game animal survey through country not regularly traversed, in which all flies taken and animals seen are assigned to every vegetational zone crossed, and the widths of the zones are either approximately measured or estimated by the time taken to traverse them.

Recovery index or Lincoln index.—The proportion of recaptures in samples from a known number of tsetses (or other animals) initially marked, to the total captured. From the recovery index under certain conditions it is possible to estimate the size of populations. *See* also p. 36 and appendix 3.

Restaurant.—Used here to describe a piece of country used by tsetses seeking food, but not for resting in. *See* " feeding-ground." Pl. 3, pl. 12, fig. 3, pl. 13, fig. 2, pl. 15, fig. 1.

rhodesiense.—*Trypanosoma rhodesiense* (Stephens and Fantham), the protozoal causative agent of the " Rhodesian " form of human sleeping sickness, carried in nature by *Glossina morsitans* and *G. swynnertoni.*

Round, fly or game.—A track marked out and divided into sections according to vegetation types, along which tsetses are collected, or game animals recorded, at regular intervals of time.

Savanna.—Grass-savanna is open grass-land (pl. 2), tree-savanna is grass-land with trees scattered as in a park (pl. 13, fig. 2, foreground), savanna wooding and savanna forest are grass-land wooded with a varyingly close stand of trees (pl. 1, pl. 3 and fig. 8).

Screen.—A rectangular piece of cloth, usually dark grey, slung lengthwise from a light pole carried between two boys, and used to attract tsetses. *See* p. 449 and pl. 7, fig. 1, and pl. 10, fig. 3; but preferably T-shaped in section. Pl. 10, fig. 2.

Secant coloration.—A type of animal coloration believed by its contrasts to afford protection against enemies by breaking up the natural form of the animal.

Shell.—*See* " puparium."

Slicing.—Separating the bark from the stump of a tree that has been felled, in order to kill it, by the method shown in fig. 27, 4. It is believed to result in fungus attack during the ensuing rains and is applicable mainly to grown acacias.

Standard climate.—The climate of a locality as measured at the ordinary open meteorological station by instruments in a Stevenson screen and outside it.

Standing catch.—*See* " drift experiment."

Street.—" A line of cover connecting coverts . . . and serving as an avenue of travel " (Leopold, 1933 : 453). We use the word runway with this meaning; runways or " streets " are shown in map 2 as connecting Block 10B with 10C.

Sub-climax.—The normal march of the vegetational succession towards the " climatic climax " may have become arrested at a particular stage by intensive grazing, regular burning, or some other inhibitive factor while the incidence of that factor persists. Such a stage may be called a sub-climax, or the responsible factor may be indicated, as (*e.g.*) in " fire climax."

Succession, plant or animal.—The natural sequence in which one plant and animal community gives place to another under undisturbed conditions until a climax is reached.

Succulent.—A plant with fleshy leaves enabling it to withstand dry conditions. Such as the bayonet-like Sansevieras in pl. 5, fig. 4, and the Euphorbia of fig. 22.

Tank, earth.—*See* pl. 16, figs. 1 and 4 and (description) p. 423.

Thorn-bush, dry.—Described on p. 89. For illustrations *see* " nyika."

Traitor species.—*See* " directive."

Transect.—One of our fly or game rounds (*see* " rounds "), or the paths from which we map vegetation (*see* Block 9 and Block 2). Our transects are in practice

belt transects, for even the tsetses come in to the observer from some distance on either side.

Vegetational concurrence.—The concurrence in a sufficiently limited area of all the vegetational types which a species, tsetse or other, needs for its feeding, resting, breeding and other requirements. *See* " edge-effect."

Vlei.—The South African term for seasonally swampy, more or less open grassland or a glade of the same character. *See* " mbuga."

Warning coloration.—Conspicuous coloration and behaviour believed to afford protection to the animal displaying it by advertising the animal's distasteful qualities or powers of offence.

Young flies.—Tsetse flies which have not yet fed since emerging from their puparia and are still soft.

APPENDIX 2.

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Note.—The " Annual Reports of the Director of Veterinary Services, Tanganyika " are listed under HORNBY; those of the " Tsetse Research Department " under SWYNNERTON; and that of the " Geological Survey Department, Uganda," under WAYLAND.

APPENDIX 3.

THE USE OF THE "RECOVERY INDEX" IN ESTIMATING THE TRUE DENSITY OF TSETSE FLIES.

By C. H. N. Jackson, Ph.D., Second Entomologist, Tsetse Research Department, Tanganyika Territory.

1. Estimation of true density.

The fundamental proposition in all work of this kind is

$$\frac{\text{flies marked week}_1 \times \text{flies marked week}_2}{\text{flies marked week}_1 \text{ and recaught week}_2} = P,$$

where P is an estimate of the total population.

Thus if we mark 1,000 flies in week$_1$, and find that, of 2,000 caught in week$_2$, there are 50 recaptures from week$_1$, it is evident that the 1,000 flies marked in week$_1$ form $\frac{50}{2,000}$ of the total population, which is therefore estimated at

$$\frac{1,000 \times 2,000}{50} = 40,000.$$

It is important to realise that this estimate is a real *true density* estimate and is *independent of the activity*, that is, the willingness of the flies to appear and be caught, since neither the number marked in week$_1$ nor the number caught in week$_2$ affects the result.

Thus, had we marked only half as many flies in week$_1$, there would have been only half as many recaptures in week$_2$. Had we caught only half as many flies in week$_2$, the recaptures would have been halved, but would have borne the same proportion to the total. In neither case would the result have been affected.

All that is assumed is that marked and unmarked flies behave alike.

But the value P is no more than an *estimate* of the total population, and, in this simple case, its accuracy is seriously affected by (i) the replacement of flies dying by flies emerging and (ii) the replacement of flies leaving the experimental area by flies coming in from outside, in the interval elapsing between marking and recapturing.

The second of these two sources of error can be eliminated by doing the experiment in a confined area into and out of which flies are unable to stray, an island for example. Suppose the experiment to be done on an island, we can get over the remaining error as follows. It is clear that, if recapturing is done at weekly intervals after the initial marking, the recaptures of flies marked will form a more or less steadily declining percentage of the total catch at every successive week of recapture, until at length no more marked flies are taken. We thus obtain a declining curve of marked flies per cent., starting from a high figure at the first week of recapture. From the mean of three or four such curves, a very smooth curve results.

In order that mean values of several curves may be obtained, as for example in the estimation of mean monthly density, all recapture figures are doubly

corrected—as if 100 flies had been initially marked in every week. Thus, if from 789 flies marked in any particular week 39 recaptures were obtained in a total of 315 marked in the week of recapture, the recapture figure would be corrected as follows :—

$$\frac{39 \times 100 \times 100}{789 \times 315} = 1{\cdot}6.$$

What one wishes to know is the corrected number of recaptures which would have been obtained had no flies died or emerged between marking and recapture; in other words, knowing the corrected recaptures for $\text{weeks}_{1,2,3}\ldots$, one requires to extrapolate the figure for week_0. It is found that the logarithms of the corrected recapture figures for the first few weeks after marking fall on a straight line; the first few points on the survival curves are therefore in geometrical progression. One can therefore extrapolate the point for week_0, the method depending solely upon the number of weeks' recaptures which one wishes to take into account for the purpose.

For a general method of extrapolation and for the calculation of the standard error of the extrapolated point I am indebted respectively to Professor R. A. Fisher, F.R.S., and to Mr. W. L. Stevens, both of the Galton Laboratory, London. A paper on the subject will shortly be written by Mr. Stevens.

After such an experiment had actually been carried out, it occurred to me that the method could be extended to unconfined areas, merely delimited by a hoed path across which flies freely come and go. In such an experiment the survival curve is of the same form but falls more rapidly, because dispersal into and out of the area are added to emergence and death respectively. An experiment on these lines was carried out during 1935. The results are still being worked out.*

It should be noted that the data can be treated in two ways. Instead of considering, as above, flies marked in any week and recaught in subsequent weeks, one can consider flies recaptured in that week and marked in previous weeks. Either method should give the same result. This is useful, because it avoids the necessity for waiting several weeks at the close of an experiment to collect recaptures of flies marked in the last few weeks. Except during the first few weeks of the experiment, the population of any week can be estimated at once.

All estimates are based in the first place on mature male flies. Young flies, which have not yet had their first meal, are differentially marked.

In the method adopted in 1935 marking is done on two consecutive days in every week, and the week of marking or recapture is shown by weekly changes of colours for both marking and re-marking. A new system, called the multiple re-mark system, has been worked out for this experiment. Flies are marked within a rectangle 1·8 square miles in area, and nearly square.

2. The "Lincoln Index."

Although I evolved the present methods independently, I was anticipated by F. C. Lincoln (May 1930, *U.S. Dept. Agric. Circ.*, **118**). Lincoln banded ducks, and found that about 12% of individuals banded were reported killed by guns in the first succeeding shooting season. From this he inferred that, banded and unbanded being killed alike,

$$\frac{\text{Total population}}{\text{Total killed}} = \frac{\text{Banded total}}{\text{Banded killed}} = \frac{100}{12}$$

*** It was found later that the average error of the monthly estimates was about 9%. A full account will shortly be published in the *Proc. zool. Soc. London*.**

or,

$$\frac{\text{Banded total} \times \text{total killed}}{\text{Banded killed}} = \text{Total population.}$$

The similarity to the formula given at the start of this appendix is obvious.

This method leaves out of account the comparatively small number of deaths from other causes between banding and the shooting season, and owing to the fact that ducks have a definite breeding season it is unnecessary to allow for the hatching of new individuals between banding and shooting. Moreover, the experiment being continent-wide, it is permissible to ignore diffusion into and out of the experimental area.

APPENDIX 4.

A SUMMARY OF SOME OF THE RESULTS OF J. D. SCOTT'S ECOLOGICAL INVESTIGATION AT KIKORE.

	% Colloid (clay)		% Organic content		Hydrogen-ion concentration (pH)		Condition in 2nd (big) rains	Holard % in wet season (total moisture content)		Holard % in dry season		Shrinkage and cracking	Surface soil temperature
	On Surface	1 ft. down	Surface	1 ft. down	Surface	1 ft. down		Surface	1 ft. down	Surface	1 ft. down		
Black alluvial seasonal swamp (open mbuga).	50%	60%	15%	10%	Just over 7 (alkaline).		Inundated.	60–100%	35–45%	2%	17%	42–48%; cracks greatly, commencing at holard 43–45%.	High, 120–150° F. after vegetation burned.
Black alluvial mbuga with (Gall-acacias) *A. formicarum*.	40%	47–56%	12%	7–10%	—		Wet to inundated.	67%	42%	2%	7%	10–20%, but very marked cracking commencing with holard at 30%.	131° F. (highest).
***Acacia Usambarensis*.**	Alluvial clay loam. 36%	45%	11%	6%	6·9 surface, slightly acid; 7·1 at 1 ft., slightly alkaline.		Inundated for short periods.	50%	23%	2%	4%	Very close-packed and hard in dry season, shrinkage very small, 6% at surface to 3% at 1 ft. down.	Under canopy seldom exceeds 115° F. 164° F. in focus spot.
***Combretum*—other species.**	Alluvial. 30–40%	45–57%	5–6%	4–5%	7·49 surface, 7·55 at 1 ft.		Very wet.	36%	32%	0·6–1%	5%	Practically no cracking, instead of a very hard cement. Shrinkage 0·3–4·3%.	Not very high. Highest recorded 124° F.
***Isoberlinia globiflora*.**	Eluvial and sandy. 12–20%	18–22%	4%	2%	7·60 surface, 6·98 at 1 ft.		Well drained.	22%	15%	0·2–0·4%	3%	Negligible, no cracking.	Seldom to 89° F. under heavy canopy up to 125° F. in exposed sites.
***Brachystegia microphylla*.**	Eluvial and sandy. 24%	—	18%	—	—		Well drained.	80%	—	1%	—	Negligible.	Seldom above 100° F.

	Permeability of soil *		Soil temperature at 1 ft.	Maximum water retaining capacity		Remarks
	Wet season	Dry season		At surface	At 1 ft.	
Black alluvial seasonal swamp (open mbuga).	Nil.	After heavy rainy season may still be quite impermeable at end of dry season.	65–83° F.	80%	40%	
Black alluvial mbuga with Gall-acacias (*A. formicarum*).	Impermeable.	Not very permeable 16–20 mins.	67–84° F.	36–41%	26–29%	
***Acacia Usambarensis*.**	Impermeable.	Great differences 4–35 mins.	64–75° F.	40%	28–30%	Unique in that at no time were the monthly temperature means at 1 ft. higher than those at 5 ft. below the ground.
***Combretum*—other species.**	Not great at either season. 47–112 mins.	45–60 mins.	70–80° F.	28–30%	30–35%	Colloid content where subsoil yellow higher than where black. Unique in M.W.R.S. being higher in subsoil and latter's permeability in dry season greater than that of surface soil. Also in porosity in the rains being greater than in the dry season. Probably due to cementing when soil dry.
***Isoberlinia globiflora*.**	Not much difference in seasons. Time taken 4 to 6 mins.		68–80° F.	45%	28%	
***Brachystegia microphylla*.**	—	—	—	Over 100%	—	Owing to shallowness, determinations of physical factors could only be made on the surface.

* Time taken for 1 litre of water to disappear into 1,000 c.c. of soil at 0·10 cm.

The factors, the measurement of which are given in the following tables, are of interest in relation to the tsetse fly not merely as deciding which types and densities of wooding will grow in particular places, but also more directly as well.

	Solar radiation temperature			Temperature ranges.				Wind	Shade and sunshine per diem, monthly mean	
	Highest max.	Lowest monthly mean	Mean monthly maxima	Highest max.	Lowest min.	Grass Minimum at 48″ Lowest	Grass Minimum at 6″ Lowest		Highest	Lowest
Black alluvial seasonal swamp (open mbuga).	—	—	Through the season. 146–160°	Wide : 91·75	to 37·5	38	33·25	Highest for any community, but maximum only 5·4 m.p.h.	7·3 hrs. per diem.	2·7 hrs. per diem.
Black alluvial mbuga with Gall-acacias (*A. formicarum*).	Higher. 164°	—	Over 140° for at least 8 months.	Wide : 94·5	to 37·0	36	37	Values low. Cut down by the trees. Highest mean over 24 hrs. = 3·07 m.p.h. after fires. Max. in Apr.–Aug. 0·36.	Similar very little shade.	
Acacia Usambarensis.	143·25	—	—	92·0 to 41·75 Less than in more exposed plots due to canopy radiation.		41	43	For short part of dry season almost as high as in open plot: maximum 4·05 m.p.h.	—	—
***Combretum*—other species.**	Seldom below 150°	—	Always above 135°	Extreme : 96·5	to 39·5	37·75	39·50	Very low. Highest max. per day 3·89 m.p.h. Highest monthly mean 3·0, lowest 0·30.	Highest under canopy of *C. Zeyheri* was 7·1 hrs. end of dry season.	Lowest 1·7 in 2nd (big) rainy season.
Isoberlinia globiflora.	157	100·0	Seldom above 135°	92·0	44·0	44	45	Cut off by trees. Highest over 24 hrs., 2·6. In April mean only 0·25.	Highest 8·4 hrs. per day with trees defoliated.	Dropped to 0·6 in wet season.
Brachystegia microphylla.	151	—	106–146	92·0	46·0	About 45	45·75	—	—	—

	(*a*) Measurements with the Eder-Hecht Graukeil photometer (Bunsen-Roscoe units). (*b*) Relative light intensity on bright sunny days at noon	Evaporation in c.c. per hour (monthly mean, October and April contrasted) At 48″ Black atmom. Oct. 1929	At 48″ Black atmom. Apr. 1930	At 48″ White atmom. Oct. 1929	At 48″ White atmom. Apr. 1930	At 6″ Black atmom. Oct. 1929	At 6″ Black atmom. Apr. 1930	At 6″ White atmom. Oct. 1929	At 6″ White atmom. Apr. 1930	Rainfall 1929–30	Rainfall 1930–31	Remarks
Black alluvial seasonal swamp (open mbuga).	Greatest mean light value for any month = 0·076 Bunsen-Roscoe units per second; lowest monthly mean = 0·021.	3·22	0·98	2·72	0·44	3·22	0·32	2·49	0·17	53·4	34·2	For month or two after fires, grass min. at 6″ lower than at 48″.
Black alluvial mbuga with Gall-acacias (*A. formicarum*).	Relative light intensity 30–70% under canopy.	2·87	0·67	2·29	0·35	3·17	0·24	2·21	0·16	46·58	29·06	Conditions severe: wind cut off by trees, canopy very slight.
Acacia Usambarensis.	13–40% at 4 ft.	2·47	0·42	2·22	0·29	2·31	0·12	1·95	0·08	In open: 44·60 Under canopy: 37·38	In open: 32·20 Under canopy: 26·46	—
***Combretum*—other species.**	100% in open. 15–50% under canopy. 0·3–1·7% under thicket.	3·14	0·77	2·44	0·42	—	0·54	2·42	0·25	In open: 47·74 In thicket: 32·69	In open: 32·00 In thicket: 28·42	—
Isoberlinia globiflora.	From 10% under canopy in wet season to 40% when leafless. 0·019 Bunsen-Roscoe units when no leaves—0·004 when in full leaf.	2·38	0·49	1·99	0·31	2·94	0·33	1·98	0·20	51·59	28·43	—
Brachystegia microphylla.	18·43% depending on season, hence canopy.	1·41 Sept.	1930 0·58	1·30 Sept.	0·39	1·46	0·48	1·15	0·32	—	31·66 under canopy.	

APPENDIX 5.

A PRELIMINARY LIST OF SOME EAST AFRICAN MAMMALS, WITH AN INDICATION OF THEIR POSSIBLE RELATION TO TSETSE FLIES.

By C. F. M. Swynnerton and G. H. Swynnerton.

Note 1. Species and subspecies, second column. The ground here covered (incompletely) comprises British and Portuguese territory from the Zambesi to the northern boundary of Kenya and Uganda.

This column has been the work mainly of G.H.S. Pitman 1935 has been referred to for Northern Rhodesian forms, personal knowledge for Tanganyika (C.F.M.S.), Roosevelt and Heller 1929 in connection with east African game animals, St. Leger 1931 in connection with the few rodents included, Sclater 1901, Shortridge 1935, Rowland Ward 1935 and the authorities of the British Museum (Natural History) in connection with all. It is hoped that the scientific nomenclature, approved by the latter, with the reservation that a number of the subspecies may yet prove invalid, will be of use to investigators.

Note 2. Under "Evidence of Food Status" is given an impression of the results of recorded blood examinations. Close deduction is not justified yet from the results of many workers differently obtained, but a single large-scale investigation of the bloods of the different species, by a standardised method and under the same conditions, may yet assist towards producing a picture of the relative usefulness of the different species of animals to the tsetse.

It is hoped also to build fully on the knowledge and suggestion summarised in the fourth column ("Contact") by means of organised observation.

Note 3. *Key to abbreviations* :—

EA—East Africa
M—Mozambique N. of Zambesi
Ny—Nyasaland
NR—Northern Rhodesia
T—Tanganyika
K—Kenya
U—Uganda
Som.—Somaliland
It.—Italian Somaliland
SS—South Sudan
Z—Zululand
Kil—Kilimanjaro
V—Lake Victoria
C—Coastal region
H—Highlands
R—river
N, S, E, W—north, south, east, west
B—bushbuck

Note 4. The vegetation and tsetse map (map 1) and the game map (map 7) should be referred to in connection with this appendix.

English name and family or sub-family	Scientific name, subspecies and distribution	Habitat	Potential contact with tsetse	Evidence of food status
Aardwolf. PROTELIDAE.	*Proteles cristatus* (Sparrm.) (Cape Province to Suakin, incl. K and T).	Mainly the dry thorn-bush and plains.	Slight. Nocturnal, in burrows by day.	None known of.
Ant-bear. ORYCTEROPODIDAE.	*Orycteropus afer* Pallas (Cape to Sudan and Somaliland, incl. *aethiopicus* Sund.). Subspp. (valid?) *O. a. lademanni* Grote (Kondoa-Irangi in T); *matschiei* Grote (Mikindani in SET); *observandus* Grote (NENy, NW Songea in T); *ruvanensis* Grote (SEV); *wardi* Lydd. (NER).	Savanna wooding generally, varying greatly in density. Not partial to rain forest.	Slight. Nocturnal, in burrows and other dark hiding-places by day.	None known of.
Baboons. CERCOPITHECIDAE.	*Papio porcarius* Sparrm. subsp. *griseipes* Poc. (L. Ngami and N. Transvaal to NR, M, and probably Ny and ST). Chacma baboon. *Papio anubis* Fischer. Subspp. (valid?) *P. a. furax* Elliot (K); *vigilis* Heller (K); *lestes* Heller (K); *neumanni* Matschie (T, Masai), and *tessellatus* Elliot (U); *doguera* Puch. Green baboon. *Papio cynocephalus* Geoff. (TC), yellow baboon. Subsp. *P. c. cynocephalus* (M, Ny, TC), synonym *P. langheldi* Matschie of NT, KC.	Most types of savanna wooding and closed forest, granite kopjes and usable cliffs.	Strong; but survival of baboons failed to procure survival of tsetses in the S. Rhodesian expt. in game destruction.	Not found infected but cannot be infected artificially. Numerous flies often found where baboons have just been and on shot baboons.

English name and family or sub-family	Scientific name, subspecies and distribution	Habitat	Potential contact with tsetse	Evidence of food status
Bat.	All genera and species.	Varies with species.	Varies; in fruit-bats hanging in foliage sometimes strong. Both bats and tsetses use hollow baobabs.	Negative, but very slight.
Bat-eared fox CANIDAE.	*Otocyon megalotis* Desm. (Cape Province, incl. Karroo, to Abyssinia).	Savanna, various, but especially the drier nyika.	Probably appreciable as partly diurnal.	None known.
Blue or Sykes Monkey. CERCOPITHECIDAE.	*Cercopithecus leucampyx*, Fischer (W. coast to Abyssinia, thence to NR). Subspp. *C. l. stuhlmanni* Matsch. (U); *neumanni* Matsch. (N. Kavirondo in K); *doggett* Poc. (SWU); *kolbi* O. Neum. (HK); *kibonotensis* Lönnb. (EK); *albogularis* Sykes (Z); *monoides* I. Geoffroy (ST); *nyasae* Schwartz (Ny); *erythrarchus* Peters (M); *opisthostictus* Scl. (NR); *moloneyi* Scl. (SWT).	Closed evergreen forest, rain forest and other.	Slight, as mainly arboreal. Perceived to feed on fruits of *Amomum*.	None known.
Buffalo. BOVINAE.	*Syncerus caffer* Sparrm. (Z to Abyssinia and generally to Lat. 15 N). Subspp. *S. c. caffer* (NR); *radcliffei* Thos. East African Buffalo (K, T, U).	All types of country not too far from water. Under persecution mainly closed forest and thicket.	Strong.	Fair proportion found infected and, on indirect evidence, a favourite.
Bush-Baby. (See Lemur.)				
Bushbuck. TRAGELAPHINAE.	*Tragelaphus scriptus* (Pall.) (throughout Ethiopian Africa to Senegambia and N. Abyssinia). Subspp. *T. s. delamerei* Poc., Highland B. (K, HT); *massaicus* Neum., Masai B. (T, eastward to long. 34; SK); *olivaceus* Hell., Coast B. (NWK); *dama* Neum., Uganda B. (U, T, NWK); *bor* Heuglin, Nile B. (NWU); *haywoodi* Thos. (K); *dianae* Matsch. (Lake T); *ornatus* Pocock (NR).	Most country with interspersal of broken or riverine thicket or closed-forest margin as rest-haunt and refuge. A stomach I examined of a bushbuck that rested regularly in rain forest contained leaves of only the shrubs and herbs of the grass-country outside (C.F M.S.).	Present but not usually abundant in most *morsitans* country. Common often in contact with *G. pallidipes* and *G. brevipalpis*.	Fair proportion found infected with trypanosomes.
Bush-pigs. SUINAE.	*Potamochoerus koiropotamus* Desmoulins (from near Capetown to Senegambia and Abyssinia). Subspp. *P. k. daemonis* Major (K, T, U); *keniae* Lönnb. (KH); *nyasae* Lönnb. (NR, Ny); *mashona* Lönnb. (M and NR ?). *Potamochaerus intermedius* Lönnb. (Semliki).	As for bushbuck; add still fuller use of high grass-jungle and the depths of unbroken closed rain forest.	Much as for bushbuck.	Seen heavily attacked by *G. pallidipes* and *G. brevipalpis*. Believed a favourite. Small proportion infected with trypanosomes.
Cane-rat. OCTODONTIDAE.	*Thryonomys swinderenianus* Temm. Subsp. *T. s. variegatus* Per. (East Cape Province to Sierra Leone and S. Sudan incl. T and NR). *Choeromys gregorianus* Thos., hind-feet partly webbed. Subspp. *C. g. gregorianus* Thos. (Kikuyu K); *pusillus* Hell. (Taita, SEK). *Ch. sclateri* Thos. (Ny).	Good grass-country, grass-jungle or reeds, in various woodland types, commonly not far from water.	Sometimes strong, perhaps partly protected by the awning of cut grass they sometimes rest under.	Blood evidence negative but scanty.
Caracal ("lynx"). FELIDAE.	*Lynx caracal* Schreb. (Mediterranean to Cape; S.W. Asia to N.W. India). Subsp. *L. c. nubicus* Fischer (K, T, U, NR generally, M).	Various types, preferably dry thorn-bush, or open country with thickets present in which to lie up.	Existent, partly diurnal. Breeds in holes (amongst rocks, in trees and burrows) in which fed and female tsetses would lie up.	Negative but scanty.
Cat (wild). FELIDAE.	*Felis ocreata* Gmelin (Cape to Mediterranean and S.W. Asia; Sardinia). Subspp. *F. o. ocreata* (K, T, U); *cafer* Desm. (NR).	As for caracal but much commoner.	As for caracal.	As for caracal.
Cheetah. FELIDAE.	*Acinonyx jubatus* Schreb. (N. Transvaal and Zululand to Lake Chad and Kordofan; S.W. Asia to Central India). Subsp. *A. j. jubatus* Schreb. (T, K, NR).	Various types woodland and open thorn-bush and plain especially.	Strong.	Fed on once, never again (exptl. evidence p. 202). Blood evidence negative but scanty.

Chimpanzee. SIMIIDAE.	*Anthropopithecus niger* E. Geoff. (R. Gambia to Congo basin to Lakes Albert and Tanganyika). Subsp. *A. n. schweinfurthi* Giglioli (SWU, Lake T).	Closed forest as a base.	Probably some contact with *palpalis* on Lake Tanganyika.	None known.
Civet. VIVERRIDAE.	*Civettictis civetta* Schreb. (N. Ngami, N. Transvaal and N. Zululand to Sierra Leone and S. Sudan, including K, T, U).	Very general.	Probably slight; strongly nocturnal, but in contact with resting tsetses by day in holes and thick bushes.	Negative, very scanty.
Colobus Monkeys. Black and White. COLOBIDAE.	*Colobus abyssinicus* Oken. (White-rumped C.; t. l. Abyss.). Subspp. *C. a. caudatus* Thos., White-tailed C. (Kilimanjaro); *kikuyuensis* Lönnb. (KH); *uellensis* Matsch. (U); *matschiei* Neum. (Rift, Elgon); *Colobus angolensis* Sclater. Subspp. *C. a. palliatus* Peters, White-shouldered C. (K, TC, Usambaras and other coast forests); *adolfi-friederici* Matsch. (SWU).	Closed forest, mainly true rain forest.	Probably nil: highly arboreal and hardly leave forest.	None.
Red.	*Colobus badius* Kerr (Sierra Leone to Congo basin, thence to K, Tana, and T). Subspp. *C. b. kirki* Gray (Zanzibar); *rufomitratus* Peters (Tana); *tephrosceles* Elliot (WU); *gordonorum* Matsch. (S. Iringa in T); *gudoriusi* Matsch. (NWT).			
Dikdiks. MADOQUINAE.				
" **Longsnouted.**	*Rhynchotragus guentheri* Thos. Subsp. *R. g. smithi* Thos. (N. Guaso Nyiro to Tana).	Grass, shrub or tree savanna *with thickets*. Wide regions of miombo are avoided: thorn-bush (nyika) and semi-desert are the main habitat. Open, thickly settled "cultivation steppe" carries a few if dense hedge-shelter is present. Water unnecessary.	Strong—where *G. swynnertoni*, *G. longipennis* or *G. pallidipes* are present.	Fed on in captivity. Deaths occur in dikdiks from country uninfested with tsetse if artificially infected.
" **Kirk's.**	*Rhynchotragus kirki* Günther (S. Somali to Shinyanga, Tabora, Ugogo). Subspp. *R. k. kirki* Günther (It.Som. and Tana R.); *minor* Lönnb. (NK); *nyikae* Hell. (EK, NET); *hindei* Thos. (K, eastward to Rift and to Kilimanjaro); *cavendishi* Thos. (T, W. of Kilimanjaro with arm N. to Baringo).			
Dog, wild. (See Hunting-dog.)				
Dormice, Grey. GLIRIDAE.	*Claviglis* spp. *Claviglis murinus* (Desmarest), Lesser African Dormouse (Cape Town to Senegal, Sudan and Somali, is in small numbers fairly ubiquitous in E. Africa).	Various veg. types, using holes in trees; live much in houses.	Nocturnal; probably nil.	None.
Duikers.				
Duiker, Common or Savanna. CEPHALOPHINAE.	*Sylvicapra grimmia* L. (Cape to Senegal, Nigeria and Abyssinia). Subspp. *S. g. shirensis* Wrought (Ny); *altifrons* Pet. (M and prob. Ny); *grimmia* L. (NR); *flavescens* Lorenz (NR); *deserti* Hell. (EK, NET); *hindei* W. (Kilimanjaro–Cen. T, Kenya–Loita); *nyansae* Neum. (WK, WT, U); *roosevelti* Hell. (NWU and SS); *urirensis* Lönnb. (NWT).	All types of savanna wooding provided good grass coverts or small thickets are present; water not vital.	Strong.	Trypanosomes found in a moderate proportion of cases.
" **Red Forest.** CEPHALOPHINAE.	*Cephalophus natalensis* A. Smith (Natal—SNy and ST). Subsp. *C. n. bradshawi* Wr. (SNy). *Cephalophus weynsi* Thos. (Belgian Congo, K, T, U). Subspp. *C. w. harveyi* Thos. (C of K and T); *ignifer* Thos. (K); *johnstoni* Thos. (U). *Cephalophus nigrifrons* Gray (Gaboon–Cameroons–Belgian Congo and K, U). Subspp. *C. n. fosteri* St. L. (Elgon); *hooki* St. L. (Mt. K).	Closed forests, whether in ravines or extensive, and thicket of various types, evergreen and dry; water available.	Existent at vegetational contacts.	None known.
" **Blue Forest.** CEPHALOPHINAE.	*Philantomba monticola* Gray. Various subspp.	Closed forest and thicket, usually under good rainfall. Drink, not always daily.	Not strong, but existent at contacts, and blue duikers often wander outside forest.	Death followed infection in laboratory.
" **Abbott's or Minde.** CEPHALOPHINAE.	*Cephalophus spadix* True (Mountain rain forests NET and Uluguru Mts. in T).	Closed forest, rain forest type, on mountains.	Probably nil.	None.

English name and family or sub-family	Scientific name, subspecies and distribution	Habitat	Potential contact with tsetse	Evidence of food status
Eland. TRAGELAPHINAE.	*Taurotragus oryx* Pall. (Ngamiland and Kruger Park—Transvaal—to Angola on W. and on E., Mongalla in S. Sudan and S. Kenya). Subspp. *T. o. pattersonianus* Lyd. (K, T, U to Mongalla on Nile); *livingstonei* Sclater (southward into South Africa from NR).	Various—plains, miombo, nyika, even light or broken thicket; can do without water.	Strong.	Tryp. infection frequent.
Elephant. ELEPHANTIDAE.	*Loxodonta africana* (Blumenbach) (Ngamiland and Olifant's River—Transvaal—to S. Sahara and N. Abyssinia. Addo Bush and Knysna in Cape). Subsp. *L. a. knockenhaueri* Matsch.; EA elephant (K, T, U).	As above when undisturbed with addition of closed forest, thicket and swamp. Where much shot, denser types mainly.	Strong.	Tryps. found.
Elephant Shrews. MACROSCELIDIDAE.	Cape to Algeria. *Macroscelides* spp.; *Rhynchocyon* spp.; *Petrodromus* spp.; *Elephantulus* spp.; *Nasilio* spp. (Transvaal to U and NK).	Closed forest, thicket, nyika, miombo, all used. Thicket or much interspersal required. *Nasilio* in dry thorn-bush.	Strong; very largely diurnal.	Certainly intolerant (exptl. evidence).
Fennec Fox. Actually Saharan. (See Bat-eared fox.)				
Fruit Bat. PTEROPODIDAE.	*Rousettus* and *Epomophorus* spp. (Cape to Egypt).	Tree savannas with thickets, riverside forest, rain forest—wherever fruit ripe.	Frequent while suspended in the day time. They collect in large numbers, often in quite low foliage.	Negative for tryps. but number examined insufficient.
Genets. VIVERRIDAE.	*Genetta* extends from the Cape Peninsula into S. Europe and W. Asia. *Genetta genetta* L. Subspp. *G. g. felina* Thunb. (NR); *hintoni* Schwarz (NR). *Genetta servalina* Puch. Subsp. *G. s. bettoni* Thos. (K, U). *Genetta tigrina* Schreb. (NR). Subsp. *G. t. stuhlmanni* Matsch. (K, T, U). *Genetta victoriae* Thos. (U).	Various tree savanna types; tree branches in thicket, hollow logs and holes by day.	Nocturnal, prob. contact in hiding-places and on commencing to move in the evenings.	Negative for tryps. but number examined insufficient.
Gerenuk, or Waller's Gazelle. ANTILOPINAE.	*Lithocranius walleri* Brooke (Somaliland and Abyssinia to N. and N.E. Tanganyika—N and EK, NT, Kil-Natron and Pare).	Nyika, some uninfested, much with *G. pallidipes* and *G. longipennis*.	Strong in some areas.	None known.
Giraffe. GIRAFFIDAE.	*Giraffa camelopardalis* L. (N. Bechuanaland, lat. 22, and E. Transvaal, 25, to Senegambia and Abyssinia, not Somali). Subspp. *G. c. infumata* Noack (Barotse); *thornicrofti* Lyd. (NR); *cottoni* Lyd. (U); *rothschildi* Lyd. (U, NWK); *tippelskirschi* Matsch. (KT); *capensis* Lesson (S of T); *G. reticulata* de Winton (NEK, It. Somali).	Plains and all types of savanna wooding, not rain forest areas.	Strong.	Tryp. infections found.
Grant's Gazelle. ANTILOPINAE.	*Gazella granti* Brooke (S.W. Dodoma to Lake Zwai, Abyssinia). Subspp. *G. g. brighti* Thos. (Rudolf-Nile, Lado); *raineyi* Hell. (NK); *robertsi* Thos. (the "Usukuma Grant," NT, SWK); *roosevelti* Hell. (mid-K); *serengetae* Hell. (the Kenya Serengeti S.E. of Kilimanjaro); *granti* (T and SK); *petersi* Günther (NCK).	Plains and nyika.	In some localities. Seldom strong owing to partiality for open spaces.	None known.
Greater Kudu. TRAGELAPHINAE.	*Strepsiceros strepsiceros* Pall. (Cape to French Congo on W., to Abyssinia in E.: not in Congo basin or to N. of it). Subspp. *S. s. bea* Hell. (T, K); *strepsiceros* Poc. (NR); *S. s. chora* Cretz. (Somali).	Various savanna types, especially nyika, provided much thicket is present of acceptable kinds. Not noted to use rain forest. Independent of water.	Strong.	Favourite: flies swarm on shot kudu and good proportion of latter carry tryps.

Hares. LEPORIDAE.	*Lepus whytie* Thos. (Ny, NR). *L. capensis* L. subsp. (NR). *L. saxatilis* Cuvier, Mountain hare (Cape to EA). *L. crawshayi* de Wint. (Kav.–Ankole). *L. victoriae* Thos. (T). *L. crispi* Brockman (It.Som.). *L. kakumegae* Hell. (Lukosa R., WK). *L. raineyi* Hell. (Marsabit in K). *L. somalensis* Heugl. (Athi Pl. in K). *Poëlagus marjorita* St. L. (Masindi, U).	Various savanna types with fair grass growth.	Appreciable in the "forms" used in the daytime, but mainly nocturnal.	Negative but slight.
	Pronolagus crassicaudatus Geoff. (Cape Province to Ny, NR), Red Rock Hare.	Mountains, kopjes and rocks.		
Hartebeests. ALCELAPHINAE.				
,, Coke's.	*Alcelaphus cokei* Günthr. (N half T to L. Baringo and Tana). Subspp. *A. c. nakurae* Hell. (Nakuru-Baringo); *kongoni* Hell. ((Guaso Nyiro and NWT, E. of Rift, KH, S. of Mt. Kenya and Naivasha); *cokei* Günthr. (broadly E. and S. Kenya, latter westward to Rift, NET west to Rift); ? *sabakiensis* Zukowsky (Athi); *ritchiei* Rux. (S. Uasin Gishu).	Nyika and other savanna woodland and ope and nearly open plain.	Existent, but largely not strong through addiction to open.	Uncertain.
,, Lelwel.	*Alcelaphus lelwel* (Heugl.) (from Bahr-el-Ghazal, Upper Nubia and Kordofan through Uganda into W. Kenya; arms through Londiani and to Mt. Kenya). Subspp. *A. l. roosevelti* Hell. and *insignis* Thos. are most in contact with tsetse in our area, former occupying a band in the Sudan and U, E. of Nile, narrowing along S.E. of Albert; the latter a broad band round W. and N. of V., thence northward to lat. 5; *jacksoni* Thos. and *keniae* Hell. lie W. of this; *lelwel* Heugl. is W. of Nile in the Sudan.	Similar.	Definitely existent.	-
,, Lichtenstein's.	*Alcelaphus lichtensteini* (Peters) (EA N. of Sabi R.—Ny, M, NR and T).	Miombo.	Strong, but appearing intolerant of the attentions of biting flies.	Smallish proportion only infected.
,, Hunter's.	*Damaliscus hunteri* (Scl.) (Jubaland to Tana R.).	Open savanna wooding.	—	—
Hedgehogs. ERINACEIDAE.	*Atelerix kilimanus* Thos. (Kilimanjaro Dwarf Hedgehog). *Aethechinus frontalis* A. Sm. (Karroo–NR–Somali).	Various, mostly (*Ae. frontalis*) in the drier areas.	Probably existent in places as incompletely nocturnal.	None.
Hippopotamus. HIPPOPOTAMIDAE.	*Hippopotamus amphibius* L. (Zambesi Watershed to Senegal and Abyssinia. Scarce now in S. Africa. All E.A. territories). On Nile typical *H. a. amphibius*; E. of Rift, *H. a. kiboko* of Heller, E.Afr. Hippopotamus.	The larger waters and grazing grounds within a mile of them.	Strong with *G. palpalis* and *G. brevipalpis*.	Used strongly by *G. brevipalpis*, used by *G. palpalis* but less than reptiles. A proportion with tryps.
Honey Badger. MUSTELIDAE.	*Mellivora ratel* Sparrm. (Cape to Senegal and Upper Nubia, K, T, U).	Various.	Fairly strong, partly diurnal. Apparently highly distasteful to mammalian predators—may be so also to tsetses.	Uncertain; to vertebrates distasteful.
Hunting-dog. CANIDAE.	*Lycaon pictus* Temm. (Cape to L. Chad, Sudan, Abyssinia and Somali). Subsp. *L. p. lupinus* Thos. E.A. Hunting-dog (K, T, U).	The various savanna types, wooded and open.	Strong; very greatly diurnal.	Fed on in captivity repeatedly.
Hyaenas. HYAENIDAE.				
,, Spotted.	*Crocuta crocuta* Erxl. (Africa generally S. of Sahara; NR). Subspp. *C. c. fisi* Hell. (K); *germinans* Matsch. (SWT).	All types.	Definite in its day haunts; partly also diurnal.	Attacked; tryps. found.
,, Striped.	*Hyaena hyaena* L. (SW Asia and NE Africa). Subspp. *H. h. bergeri* Matsch. (NK); *dubbah* Meyer (K, NT); *schillingsi* Matsch. (NET).	Mainly the dry thorn-bush (nyika) country.	The same.	Uncertain.
,, Brown.	*Hyaena brunnea* Thunb. (Bechuanaland, Transvaal, Zulu, to, sporadically, M, Ny, NR, T and K).	—	—	—

English name and family or sub-family	Scientific name, subspecies and distribution	Habitat	Potential contact with tsetse	Evidence of food status
Hyrax. PROCAVIIDAE.	*Procavia* Storr (Cape Peninsula to Upper Egypt and Abyssinia). *P. matschiei* Neum. (Mwanza, S. end of V). *P. ituriensis* Brauer (Ituri). *P. jacksoni* Thos. (Ravine Station. K). Subsp. *daemon* Thos. (Mt. Elgon, 7,000 ft., and Kisumu, K). *P. johnstoni* Thos. (Ny). *P. mackinderi* Thos. (Teleki Valley, Mt. Kenya). Subsp. *zelotes* Osgood (typ.-loc. between Naivasha and Kijabe, K). *P. mima* Thos. (Ny–T plateau; NNy). *P. sharica* Thos. and Wrought. (Kajibu, Shari R., L. Chad district). *Dendrohyrax* Gray (E. Cape Province to K and U, and to Senegambia). *D. arboreus* A. Smith (Zambesi to Natal, including M and SEK, Taita Hills). *D. bettoni* Thos. and Schw. (Rogaro, Kikuyu, mile 346 on U rly., K). *D. crawshayi* Thos. (typ.-loc. W. slope of Mt. K. Another from Roromo, Kikuyu Forest). Subsp. *laikipia*, Dollm. (Laikipia plateau, K). *D. marmotta* Thos. (Mengo, N. of Entebbe, S. of Kampala, U). *D. terricola* Mollison (E. Usambara, coast opp. Zanzibar. Subspp. *schusteri* Brauer (Uluguru Mts., T); *vosseleri* Brauer (Sigi, nr. Amani, T). *D. neumanni* Matsch. (Zanzibar; also Pangani Forest, T). *D. ruwenzorii* Neum. (Ruwenzori, U, 11,000–11,500 ft.). *D. scheelei* Matsch. (Khutu, Ruaha Valley, T). *D. scheffleri*, Brauer (Kilwezi, K). *D. stuhlmanni* Matsch. (Bukoba, V, Burumba, Ankole, Shinganya). *Heterohyrax* Gray (N. Transvaal to Abyssinia). *H. brucei* Gray (Abyssinia, Som., U, Ugogo, T, etc., to M). Subspp. *albipes* Hollister (typ.-loc. Telek R., Loita Plains, K); *bakeri* Gray (typ.-loc. Latiko, U); *borana* Lönnb. (N. of N. Guaso Nyiro, above Chanler Falls, Bora district, Mt. Lololokwi); *dieseneri* Brauer (Ushashi, Guta on Speke Gulf, V, Ikoma, Geri, Serengeti Plains, and Ukerewe Island); *hindei* Wrought. (typ.-loc. Fort Hall, Kikuyu Country, K); *kempi* Thos. (typ.-loc. Mt. Elgon, 7,000 ft.); *maculata* Osgood (typ.-loc. Lukenya Mtn., K, Athi); *manningi* Wrought. (typ.-loc. Mlanji, Ny.); *prittwitzi* Brauer (Dodoma dist., T); *ruddi* Wrought. (Gorongoza Mtns., M); *victoriae-njansae* Brauer (Nyangezi, Mwanza, Mondo, Shinyanga, T). *H. frommi* Brauer (Mahenge, T). *H. lademanni* Brauer (Livingstone Mtns., nr. Mwakete, 2,040 m. above L. Nyassa).	Rock piles in all types of country. *Dendrohyrax stuhlmanni* in rain forests and (lately noted) niyka wooding.	In the rock piles, low down, much probable contact with *G. swynnertoni*.	Blood examination negative, quite likely intolerant.

	H. münzneri Brauer (Kasanga, LT). Subsp. *rukwaensis* Brauer (L. Rukwa and Rudshergi Post, Lake T). *H. pumila* Thos. (Som.). Subsp. *rudolfi* Thos. (N. end L. Rudolf, N. of N. Guaso Nyiro, below Chanler Falls). *H. schubotzi* Brauer (N. of L. Kivu, Bugoya Forest).			
Impala. AEPYCEROTINAE.	*Aepyceros melampus* Licht. (Orange River to U and K on E., to Angola on W.). Subspp. *A. m. suara* Matsch., Equatorial Impala (NT prob. U); *johnstoni* Thos. (Ny, M, NR and prob. ST); *rendilis* Lönnb. (K).	Savanna wooding or scattered thicket with interspersion of open grassy spaces, large and small. Open used on persecution by wild animals and in evenings; thicket under severe persecution by man—never rain forest.	Strong.	Blood result often positive.
Jackal, Side-striped. CANIDAE.	*Canis adustus* Sund. (Ngamiland, Transvaal, Zululand to Kenya; Ny, NR, M, T, K, and prob. SU). Subspp. *C. a. bweha* Hell. (K); *notatus* Hell. (K, T).	Various.	Fair, being quite largely diurnal.	Blood examinations negative but few.
„ **Black-backed.**	*Canis mesomelas* Schreb. (Cape Flats to Middle Nubia, nearly omitting Zambesia; all over E. Africa, T, K, U, Som.).	Various.		
Klipspringer. OREOTRAGINAE.	*Oreotragus oreotragus* Zimm. (Abyssinia and Nigeria to Cape Peninsula). Subspp. *O. o. oreotragus* (NR); *aureus* Hell. (NK); *schillingsi* Neum. (SK and T).	Granite kopjes and tops, other rock piles, even small, and negotiable cliffs.	Existent but usually weak.	None known.
Kob, Equatorial. REDUNCINAE.	*Adenota kob* (Gray) (Senegal and Niger to Nile and V). Subspp. *A. k. alurae* Hell., Lado Kob (L. Albert and Southern Bahr-el-Ghazal drainage); *A. k. thomasi* Neum., Uganda Kob (U, WK).	Grassy plains not far removed from water.	—	—
Kudu.	See Greater and Lesser.			
Lechwe. REDUNCINAE.	*Onotragus leche* Gray. Subspp. *O. l. leche* (Zambesi, Ny and NR); *smithemani* (Bangweolo, NR).	Extensive permanent swamps.	—	—
Lemur. GALAGIDAE. „ **Large Grey.**	*Galago crassicaudatus* Geoffr. (Natal and Zoutpansberg northward, and throughout Tropical Africa). Subspp. *G. c. crassicaudatus* Geoffr. (Moz.); *panganiensis* Matsch. (T except C); *monteiri* Gray (Ny, SWT, NR); *lasiotis* Ptrs. (K, T, It.Som.); *kikuyuensis* Lönnb. (K inland); *agysymbanus* Coquerel (Pemba, Z).	Most woodland types where figs and other fruits are abundant, although very greatly insectivorous.	Sleep high in the day, contact small.	Blood examination negative, but insufficient.
„ **Bush-Baby.**	*Galago senegalensis* Geoff. (Ngamiland and S. Transvaal to Senegal and Somaliland). Subspp. *G. s. braccatus* Elliot (HK and T to Pangani); *moholi* A. Smith (ST and NR); *albipes* Dollm. (K) and others.	Riverine wooding and miombo.	In holes by day, contact with resting tsetse occasionally possible. Fur a probable protection.	
Leopard. FELIDAE.	*Panthera pardus* (L.) (practically throughout Africa and Southern Asia and China). Subspp. *P. p. centralis* Lönnb. (Cen. Afr.); *suahelica* Neum., E.A. Leopard (K, T, U); *chui* Hell. (NU) Nile Leopard; *fortis* Hell. (K), Mau Leopard; *nanopardus* Thos. (Somali).	Closed forest and all types of savanna with any thick cover interspersed.	Perhaps strong with *G. pallidipes*, *G. swynnertoni*, *G. austeni*, and *G. brevipalpis*, with *G. morsitans* less but appreciable.	A positive blood result.

English name and family or sub-family	Scientific name, subspecies and distribution	Habitat	Potential contact with tsetse	Evidence of food status
Lesser Kudu. TRAGELAPHINAE.	*Strepsiceros imberbis* Blyth (Somali to K and T). Subsp. *S. i. australis* Hell., E.A. Lesser Kudu, (Abyssinia, Som. N and EK, T, Masailand and Pare and S. to S.E. Dodoma).	Based on dense cover in the drier thorn-bush (nyika) area.	Probably strong in the sections infested by *G. swynnertoni*, *G. pallidipes*, *G. longipennis*.	None known.
Lion. FELIDAE.	*Panthera leo* L. (Algeria to Cape). Subspp. *F. l. massaica* Neum., E.Afr. Lion (K, T, U); *nyanzae* Hell., Uganda Lion (T west of V, U); *hollisteri* J. Allen (K).	All vegetational types but rarely *extensive* closed forest. Lying-up cover of thicket, reeds or long grass.	Strong.	Positive blood results.
Mangabey, Grey. CERCOPITHECIDAE.	*Cercocebus galeritus galeritus* Peters (Tana). Black Mangabey *C. albigena johnstoni* Lyd. (Upper Congo to U, Urundi and L. Mweru, NR).	—	—	—
Mice.* MURIDAE.				
„ Tree.	*Dendromus* spp. (Cape Town to Cameroons and Kenya). (*D. whytei* Wrought., Ny and K; *D. insignis* Thos., K). *Poemys* spp. (Cape to Nigeria and Kil). (*P. nigrifrons* True (Kil and K)).	Thicket, reedbeds, grass-jungle or forest outskirts, trees. *Poemys*, less generally arboreal, in long tangled grass near vleis but also "in bush country and thin timber along streams" (Heller).		Blood examinations of MURIDAE many, negative; highly susceptible to artificial infection. Probably very intolerant.
„ Fat.	*Steatomys pratensis* Ptrs. (Natal to Mozambique and S. Congo, NR); *S. athi* Hell. (K).	Burrows in sandy ground in savanna forest incl. mopane.		
„ Shamba.	*Mastomys coucha* A. Smith (Cape to Morocco and Abyssinia, locally abundant).	Rank cover and cultivation, partly diurnal.		
„ Many-striped Grass.	*Lemniscomys* (*Arvicanthis* group) (Zululand to N. Africa–Morocco, etc.) (*L. barbarus* L., K, T; *L. striatus massaicus* Pagenstacher L., K; *L. griselda* Thos., one-striped. K).	Vleis.	With *Mastomys*, *Lemniscomys* and *Arvicanthis*, savanna-dwellers moving largely diurnally in tsetse feeding-grounds, the contact is probably strong.	
„ Four-striped Grass.	*Rhabdomys pumilio* Sparrm. (S and EA gen.).	Scrub and long grass near river-beds, water-holes and forest margins.		
„ Gerbil.	*Gerbillus* spp. (Small gerbils). *Taterona* spp. (Large gerbils). (Cape Peninsula to Gambia and Nubian desert). (*T. nigrita* Wrought. (U); *T. liodon* Thos. (NR, K, U); *T. vicina* Peters (K, T); *nigricauda* Peters (K and Mt. Elgon to Abyssinia)).	The drier savannas—*Gerbillus* especially.	Nocturnal.	
„ Pigmy.	*Leggada* spp. (*L. bella*, Thos., subspp. Zululand to Abyssinia; *L. grata* Thos. (K, WU); *L. triton* Thos. (K and Mt. Elgon); *L. tenella* Thos. (K)).	"Fairly damp country, not far from water," where there is cover (Shortridge).	Nocturnal.	
„ Grey dormouse.	See Dormouse.			

Mongooses. VIVERRIDAE.				
„ Banded.	*Mungos mungo* Gmel. (N.E. Cape Province to N. Nigeria, Sudan, Abyssinia). Subspp. *M. m. colonus* Hell. (K); *macrurus* Thos. (WU); *mungo* Gmel. (NR).	All veg. types including closed forest.	Strong; abundant in tsetse country in conspicuous parties, and diurnal.	
„ Large Grey.	*Herpestes cafer* Gmel. (Knysna to M, Ny, NR, K, T, U—further north, in form of *H. ichneumon*, into Spain).	Most woody vegetational communities not very far removed from water.	Existent; partly diurnal and lies up when at rest in potential tsetse resting-places as under overleaning trees and between exposed root-bases.	
„ White-tailed.	*Ichneumia albicauda* (Cuvier) (E. Central Cape Province to Abyssinia, Sudan, Senegal). Subspp. *I. a. albicauda* Cuv.; *dialeucas* Hollister (K); *ferox* Hell. (K); *ibeanus* Thos. (K); *leucura* Hempr. and Ehr. (K, T, U).	All permanent swamps and waters including Lake Victoria, but also dense forest and savanna wooding where thicket is available in the latter, even some miles from permanent water as at Shinyanga.	Nocturnal.	
„ Marsh.	*Atilax paludinosus* Cuv. (from Knysna in the Cape Province through the greater part of Africa, South of the Sahara, incl. Ny, NR, T, U).	Water-margins—aquatic.	With *G. palpalis*, though largely nocturnal.	None yet known, all mongooses probably intolerant.
„ Black-tip-tail Slender.	*Myonax cauui* A. Smith (Orange River and the Transkei through most of Ethiopian Africa). Subspp. *M. c. cauui* A. Smith, and *M. c. lancasteri* Roberts (NR).	Ubiquitous singly but shy. Savanna woodland with thickets.	Probably existent, diurnal.	
„ Little.	*Helogale parvula* Sundevall, and allies (Natal to Italian Somaliland). *Helogale victorina* Thos. (V.). Subspp. *ochracea* Thos. (Ankole in U). *H. varia* Thos. (NNy). *H. brunnula* Thos. and Schwann (Ny, NR). Subspp. *ruficeps* Kersh. (NWR) and *undulata* Peters (K, T, M and NR). Other species are *vetula* Thos. (Lamu in K); *hirtula* Thos. (Somali); *percivali* Thos. (NK). subsp. *ahlselli* Lönnb. (N. of N. Guaso Nyiro in K).	Savanna wooding, open or close, with thickets or scrub.	Habits like those of the banded mongoose.	
„ Meller's.	*Rhynchogale melleri* Gray (NR).			
Monkeys.	See Colobus, Blue, Mangabey and Vervet.			
Oribi. NEOTRAGINAE.	*Ourebia cottoni* Thos. and Wrought. (K, T, strips S. and E. of V. and northwards). *O. haggardi* Thos., Coast Oribi (K, T). *O. kenyae* Meinertzh. (Mt. K). *O. montana* Cretz. Subsp. *O. m. aequatoria* Hell., Nile Oribi (NU, Sudan). *O. ourebi* Zimm. (S. Afr. up to Zambesi and NWR). Subsp. *O. o. hastata* Peters (M to Ny). *O. pitmani* Rux., Pitman's Oribi (U).	Mbugas, plains and other open spaces, on hills or on the flat, enclosed in woodland or otherwise.	When in margins of open spaces in definite contact; much out of contact also.	A few positive blood examinations.
Oryx. ORYGINAE.	*Oryx beisa* Rüpp. (Eritrea to T). Subspp. *O. b. annectens* Hollister, Ibean Oryx (Laikipia, K); *callotis* Thos., Fringe-eared Oryx (Kenya S. of Ulu to Rift and (E. of Rift) S. to Mpapwa); *subcallotis* Rothsch. (Central K).	The drier nyika and its plains.	Existent, sometimes strong.	None known.
Otters. MUSTELIDAE. Great Clawless. Lesser, Spotted necked.	*Aonyx capensis* Schinz (EA generally). *Lutra maculicollis* Lcht. (EA generally).	Most waters with appreciable fish.	With *G. palpalis*.	Several examined; negative.
Pangolin. MANIDAE. Lesser. Greater.	*Manis tricuspis* Raf. (K, T, U). *M. gigantea* Ill. (Central and EA).	Various; well distributed though scarce and seldom seen.	Definite, partly diurnal.	None known; much body-surface protected.

* A selection only. See also Rats. Other E. African mouse-genera are in any case for the most part nocturnal.

English name and family or sub-family	Scientific name, subspecies and distribution	Habitat	Potential contact with tsetse	Evidence of food status
Peter's Gazelle.	See Grant's Gazelle.			
Pigmy Antelope or Suni. NEOTRAGINAE.	*Nesotragus moschatus* von Duben. Subspp. *N. m. moschatus* (islands off Zanzibar); *N. m. akeleyi* Hell., Highland Suni (K mountains); *deserticola* Hell., Coast Suni (K and NT); *kirchenpauri* Pagenstecher, Kilimanjaro Suni (T).	Closed forest (*akeleyi* and *Kirchenpauri*) and coastal thickets (*deserticola*), feeding in the more open grass-glades.	Certainly (*deserticola*) with *G. pallidipes*, *G. austeni*, *G. brevipalpis*.	None known.
Porcupine. HYSTRICIDAE.	*Hystrix africae-australis* Ptrs. (K, T, U).	All well-drained types, more or less, where rock-holes available or dry holes can be dug.	Strong.	Blood examinations negative but few.
Puku. REDUNCINAE.	*Adenota vardoni* Livingstone (Zambesi valley to T—M, Ny, NR, U).	Open spaces and plains, by large rivers, seasonally or more permanently inundated.	When near the margins of the wooding.	Some positive blood examinations.
Putty-nose Monkey. CERCOPITHECIDAE.	*Cercopithecus nictitans schmidti* Matschie (U). *C. neglectus* Schlegel also occurs (Kavirondo in K).	—	—	—
Rats. MURIDAE.				
„ Giant Pouched.	*Cricetomys gambianus* Waterhouse (N. Transvaal to Senegambia and S. Sudan, incl. M, K, T and NR).	High forest and thickets in more open forest, in burrows by day.	Probably slight, but to some extent existent, as partly diurnal.	Examination negative but one only.
„ Vlei.	*Otomys irroratus* Brants (Cape Province to Cameroons and Abyssinia); *O. denti* Thos. (Ruwenzori E.), *tropicalis* Thos. (K and Elgon); *angoniensis* Wrought. (N); and *Dasymys* (Zululand to Sudan and N. Nigeria); *D. bentleyae* Thos. (K, U).	"Vleis, swamps and reed-fringed river beds" (Shortridge). "Moist, open grass-places" (Heller).	The same.	—
„ Cane.	See Cane Rat.			
„ Tree.	*Thallomys* (Orange River and Zululand to K). *T. damarensis* de Winton (Ny); *T. loringi* Hell. (K); *T. scotti* Thos. and Hinton (K).	Large trees in savanna or near water.	Nocturnal but in tree-holes which tsetses may sometimes use if low.	—
Ratel.	See Honey Badger.			
Reedbucks. REDUNCINAE.				
„ Bohor.	*Redunca redunca* Pall. (W. Africa, E. Africa, Abyssinia to NR). Subspp. *R. r. cottoni* Roths., Nile R.b. (NU and White Nile to W. Somali); *tohi* Hell., Coast reedbuck (KC narrowly, TC broadly); *ugandae* Blaine, Ankole R.b. (U); *wardi* Thos. EA. Highland reedbuck (K, SU, NT). Last three perhaps all really *R. r. wardi*.	Open or semi-open mbuga, plain or grassy hillside, with interspersal of reed or long grass coverts.	In many places existent or strong.	Moderate proportion shows trypanosomes.
„ Southern.	*Redunca arundinum* Boddaert (Cape to Angola and South T, incl. M, Ny, NR). In NR subsp. *C. a. occidentalis* Roths.	Similar.	As for *redunca*.	
„ Mountain.	*Redunca fulvorufula* Afz. (Natal to K). Subsp. *R. f. chanleri* Roths. Chanler's Mountain Reedbuck (Hill country K and T).	Grassy hillsides and tops, open to fairly open.	Generally less than for *redunca* and *arundinum*.	None known.
Rhinoceros, black. RHINOCEROTIDAE.	*Diceros bicornis* L. (formerly Abyssinia to Cape, now, S. of Zambesi, only in scattered localities). Subsp. *D. b. bicornis* L. (NR, T, K to Tana, NU)—including *D. b. holmwoodi* Sclater (K), *somaliensis* Potocki (E. and N. of Rudolph and Tana).	Nyika and plains, and miombo, especially former: closed forest and dense thicket.	Strong.	Readily fed on, blood examinations few.
Roan Antelope. ORYGINAE.	*Hippotragus equinus* Desm. (E. Transvaal to Sudan, Angola-Senegambia). Subspp. *H. e. equinus* Desm. (M, Ny, NR); *langheldi* Matsch., E. African roan (T, K, U); *rufopallidus* Neum. (? T, K); *bakeri* Heugl., Nile Roan (NWU, Sudan).	Nyika and plains, and miombo, west of the Rift in Tanganyika and, again, back of Bagamoyo. In disconnected localities in Kenya.	Strong.	Proportion infected.

Rock-Rabbit.	See Hyrax.			
Sable. ORYGINAE.	*Hippotragus niger* Harris (N. Transvaal to Angola and SEK). Subspp. *H. n. niger* Harris, Southern Sable (M, Ny, NR), and *roosevelti* Hell., E.Afr. Sable (T, SEK).	Miombo and its equivalents.	Strong.	Small proportion found infected.
Scaly Ant-eater.	See Pangolin.			
Serval Cat. FELIDAE.	*Leptailurus serval* (Schreber) (practically all Africa S. of Sahara, incl. NR, K, T, U).	Various.	Existent, though mainly nocturnal.	None known.
Situtunga. TRAGELAPHINAE.	*Limnotragus spekei* Sclater (main waters of Central, S. Central and E. Africa). Subspp. *L. s. selousi* Rothsch., Southern Situtunga (NR, Ny); *spekei* Scl., Eastern Situtunga (K, T, U—lakes and main swamp rivers entering them).	Papyrus swamps mainly; in the absence of man, wooding and open grass-land near water.	Strong with *G. palpalis*.	Proportion infected: readily fed on.
Shrews. SORICIDAE.	*Crocidura* and other genera.	Various: several species inhabit river banks and the borders of swamps.	Probably just existent but shrews are very intolerant (experimental evidence).	Examinations negative, few examined.
Spring-Hare. PEDETIDAE.	*Pedetes caffer* Smith (Cape to NR, not found in Ny and M). *P. surdaster* Thos. (T and K).	Miombo and drier communities; very local.	Small: nocturnal, in burrows by day.	None known.
Spotted Hyaena.	See Hyaena.			
Squirrels. SCIURIDAE.	*Funisciurus* spp., *Heliosciurus* spp., *Paraxerus* spp., *Xerus* (Ground Sq.).	Several of the squirrels live in closed forest, some, as *P. capapi*, in savanna wooding, *Xerus*, ground-squirrel, likes more open country.	Small in most, doubtless present in some as *P. apapi sindi* Thos. and Wrought. of Mopane Woods in NR (Pitman).	Examination negative but insufficient examined.
Steinbucks. NEOTRAGINAE.				
„ Common.	*Raphicerus campestris* Thunb. (S. Africa, incl. Cape, S. Angola, scarcer in M. and Ny). Subspp. *R. c. neumanni* Matsch. (K–N to Elgon, and T); *stigmatus Lönnb.* (Natron).	Several savanna types, especially common in the thorn-bush with some bush or scrub cover. Often far from water.	Strong.	Uncertain.
„ Sharpe's.	*Raphicerus sharpei* Thos. (S.W. Africa and Swaziland to T). Subsp. *R. s. sharpei* Thos. (Ny, NR, ST).	Mainly miombo.	Strong.	
Striped Hyaena.	See Hyaena.			
Suni.	See Pigmy antelope.			
Sykes Monkey.	See Blue monkey.			
Thomson's Gazelle. ANTILOPINAE.	*Gazella thomsoni* Günthr. (Shinyanga to the Pangani R., Baringo to Ruaha R). Subspp. *G. t. thomsoni* Günthr. (mid SK, mid NT); *nasalis* Lönnb. (mid K, NWT).	Thorn-bush (nyika) with openings and especially open plain.	Moderate only owing to partiality for open spaces.	None known.
Topi. ALCELAPHINAE.	*Damaliscus korrigum* Matsch. (two discontinuous areas—KC and WT and K with arm from Kavirondo to near Nimule). Subspp. *D. k. eurus* Blaine (T); *jimela* Matsch. (KT); *selousi* Lyd. (K); *topi* Blaine (K); *ugandae* Blaine (WU); *tiang* Heugl. (L. Albert, NU and Sudan).	Miombo (in west T), thorn-bush and open plain west of the Rift, and again on the lower Tana.	Strong in miombo, existent in the thorn-bush, reduced by partiality for open plains.	A proportion infected.
Tsessebe. ALCELAPHINAE.	*Damaliscus lunatus* Birch (Orange River to Ngamiland and NR, Ny and NR).	—	—	Examination negative but few examined.
Vervet Monkey. CERCOPITHECIDAE.	*Cercopithecus aethiops* (L.) (Cape to Senegambia and Abyssinia in N. and Pemba and Manda Is., in E). Subspp. *C. a. centralis* O. Neum. (U); *johnstoni* Poc. (K, NT); *callidus* Holl. (Naivasha); *rufoviridis* O. Neum. (M and Angoni, Ny); *nesiotes* Schwarz (Pemba); *arenarius* Hell. (NK); *cynosuros* Scopoli (NR).	The various savanna tree communities.	Strong, but intolerant.	Large numbers examined, results negative: easily infected artificially.

English name and family or sub-family	Scientific name, subspecies and distribution	Habitat	Potential contact with tsetse	Evidence of food status
Wart-Hog. SUIDAE.	*Phacochoerus aethiopicus* Pall. (Natal to Abyssinia and Senegal). Subspp. *P. a. massaicus* (Kilimanjaro); *sundevalli* Lönnb. (NR); *aeliani* Cretzschmar, E.Afr. Wart-hog (Abyssinia to K, U, and T); *P. a. bufo* Hell. The Nile Wart-hog (falls just outside our area in the Sudan). *P. a. delamerei* Lönnb., Desert Wart-hog (Lower drainage area of N. Guaso Nyiro R in K), lacking incisors in either jaw, resembles typical *P. aethiopicus* Pall. of the Cape.	Most types of savanna wooding.	Strong.	A proportion infected.
Waterbuck. REDUNCINAE.				
„ Defassa.	*Kobus defassa* Rüppell. Subspp. *K. d. crawshayi* Sclater (NR); *raineyi* Hell. (K, T); *ugandae* Neum. (K, T, U).	Savanna wooding of most types and long-grass savanna near the larger permanent waters.	Strong.	A large proportion infected.
„ Common.	*Kobus ellipsiprymnus* Ogilby (Zululand to Italian Somaliland incl. M, Ny, NR, T, K). Subspp. *K. e. kuru* Hell. (KC, TC and Pangani and Tsavo River areas); *thikae* Matsch. (Cen. T and Cen. K with extension along North Guaso Nyiro and Tana Rivers).			
Weasels. MUSTELIDAE.				
„ Lesser (Afr. Striped Weasel).	*Poecilogale* extends from the Cape Province to T. *Poecilogale doggetti* Thos. (SWU), and *Poecilogale albinucha* Gray (WT, Bukoba).	Most types.	Probably nil: nocturnal and spends day in holes. Probably highly distasteful to carnivora.	None known, has a fetid discharge and may be highly unpalatable.
„ Greater (Zorilla-Striped Pole-cat).	*Ictonyx* extends from the Cape to N. Africa except Sahara and perhaps Congo forests. *Ictonyx striatus* Shaw. Subspp. *I. s. striatus* Lay. (T); *lancasteri* Roberts (NR).			
Wild Cat.	See Cat.			
Wild Dog.	See Hunting Dog.			
Wildebeests. ALCELAPHINAE.				
„ Blue, or Brindled.	*Gorgon taurinus* Burchell (Vaal River to Kenya). Subspp. *G. t. taurinus* Burch. (NR); *cooksoni* Blaine (NR); *johnstoni* (M, Ny, ST).	Plains and open spaces in thorn-bush and (on alluvium) in miombo areas.	Often appreciable: would be stronger were it not for addiction to open plains.	A proportion infected.
„ White-bearded.	*G. t. albojubatus* Thos., Eastern White-bearded wildebeest (K and T, E. of Rift). Subspp. *mearnsi* Hell. Western White-bearded wildebeest (K and T, W. of Rift).			
Zebras. EQUIDAE.				
„ Common or Bonte-Quagga.	*Equus quagga* Gmel. (S.W. Africa to Benguella, Zululand to Lake Zwai, Abyssinia). Subspp. *E. q. zambesiensis* Prazak, Zambezi Zebra (NR); *granti* de Winton, Highland Zebra (U, WK to Ulu incl., WT to Arusha); *boehmi* Matsch., coast Zebra (KC, TC to Kilimanjaro incl. and Mkata); *cunninghamei* Hell. Desert Quagga Zebra (NEK).	Most savanna types, with a strong partiality to the open and semi-open spaces and plains.	Appreciable: would be stronger were it not for addiction to open plains.	A proportion infected, but some evidence that rather avoided by tsetse.
„ Grévy.	*Dolichohippus grevyi* Oustalet, Grévy's Zebra (K, N. of Tana and E. of Rudolph, with arm to L. Zwai in Abyssinia; and in Somaliland).			

APPENDIX 6.

THE VERNACULAR NAMES OF EAST AFRICAN MAMMALS.

By C. H. N. Jackson, Ph.D., Second Entomologist, Tsetse Research Department, Tanganyika Territory, and A. Loveridge.

English	German	Afrikaans	Masai	Zulu and Shangan-Zulu	Kiswahili	Kisukuma	Kinyamwesi	Kinyaturu	Kirangi	Kisandawe	Chigogo	Kizigua	Kisagara	Kisungwa	Kn Bukoba
Aardwolf	Erdwolf	Aardwolf or Maanhaar	—	—	kungugua or fisi mdogo	pitimlulu	kakonko-gombe	mpiti-mongu	—	bugwili	—	—	—	—	—
Ant-bear	Kapschwein, Erdschwein, Erdferkel	Erdvark	—	Isambane	muna-ng(w)a	naga	nyaga	ngaya	muha-nga	gqena	nyamuhanga	—	—	—	—
Baboon, Green / **Yellow**	Grüner Pavian / Gelber Pavian	Baviaan or Bobbejaan	Ol l'Ngaima	Ifene (Sh.) or imfena	nyani	guku	iguku or nkobi	poma	chwe	xoxa	mhuma	—	nyabu	nyabu	—
Bat	Fledermaus	Vlermuis	—	—	popo	tunge	litunge or tuvugu-lima	tai	kinkuro-nkuro	tari	ibudibudi	—	—	—	—
Buffalo	Büffel	Buffel	Ol Osogwān	—	nyati, 'mbogo	mbogo	mbogo	mbowe	mboo	caeu	mbogo	mbogo	mbogo	mbogo	Mbogo
Bushbuck	Busch-Bock	Boschbok, Bosbok	Sarga or El Mungu (H)*	Mbabala (Z), Ishoma (Sh.)	mbawala mbala or mba-rawara	mhongo	mpongo or mhongo	—	mbavala	bá-asa	mbala	mbala	mba-wala	mato	ngabi
Bush-pig	Fluss-Sumpf-schwein	Bosvark	—	Ngulube	nguruwe	gurube or numba	ngurube or mumba	nguma	nguruwe	géudo	njegere or ngubi	—	ngubi	ngubi	mpuno
Cane-Rat	Rohrratte	Rietmuis, Rietrot	—	Ivondwe or Ivondo (Sh.)	ndezi	kashenzi	senzi or senji	—	mancho-ru	—	ndezi	—	—	—	—
Caracal or lynx	Karakal	Rooikat	—	—	njusi or simba-mangu	nangu	mbwama-nsi or mangu	? njuli	simba-mnyo-ngi	mangoo	simba mwe-ngwe	—	—	—	—
Cheetah	Gepard	Jagluipard	Engingilasho (H)	Ngulule or Nhlozi (z)	duma	nzoli	simba-ngwe or uvala-wala	jori	lusi	jori	duma	—	dula-nyenge	—	—
Chimpanzee	Schimpanse	Sjimpansee or Mansaap	—	—	soko	—	tanda	—	—	—	—	—	—	—	—
Civet	Zibethkatze	Sivet or Mus-keljaatkat	—	Ivungu	fungo	nhungo	tunge, litungo	tungo	—	nima	fungo	—	fungo	fungo	—
Colobus Monkey	Weisschwanz-Seidenaffe	—	—	—	mbega	—	Mkunga	—	—	—	mbega	mbega	—	—	—
Dikdik	Windspiel-antilope	Neusbok	Engaimani (H)	—	suguya	suguya	suguya or Mburu-nga	ngu-uya	vudu	cia	chizimba	npala	zimba	tsimba	—

* Denotes Masai names taken from Roosevelt and Heller, 1929.

English	German	Afrikaans	Masai	Zulu and Shangan–Zulu	Kiswahili	Kisukuma	Kinyamwesi	Kinyaturu	Kirangi	Kisandawe	Chigogo	Kizigua	Kisagara	Kisungwa	Kn Bukoba
Dog, Wild. See Hunting Dog															
Duiker, Common or Savanna	Ducker-Antilope	Duiker	E'mbutuwin	Mpunzi	nsha, funo	—	kasya or subuya (L)	mia	nsya	gqaka	haluzi	funo or dondolo	kidundugo	—	—
,, Red Forest	Schopf-antilope	Rooi-bos-bokkie	—	Mkumbi	funo or nsha	—	kasya	—	—	—	fulo	—	—	—	—
,, Blue Forest	—	Bloubokkie	—	Ipiti	paa	—	—	—	—	—	ndimba	—	—	—	—
,, Abbott's or Minde	Mindebock	—	—	—	minde	—	—	—	—	—	—	—	—	—	—
Eland	Elenantilope	Eland	O'Sirrwa	impofu	mpofu	mboku	nyimba	poku	poku	qo-a	nhongolo	npofu	pofu	Tongolo	ntamu or nskwaga
Elephant	Elefant	Olifant	Ol Tóme Ol chángito Sabuk, sometimes Ol l'ngaîna (he of the hands)	indhlovu	tembo or ndovu	mhuri	njovu or mhuri	njoo	njoo	cwaa	nhembo	ntembo	tembo	tembo	njoju
Elephant Shrew	Elephantem spitzmaus	Skeerbek-muis	—	nyakou (Sh.)	sange	bulu	lisenge	ngyenge	nyala	nangese	mbulusange (*Rhynchocyon*) nghulumwaga (*Petrodromus*) mbulu (*Elephantulus*)	—	sange nimbo liwaki	sange doroga doroga	—
Fruit Bat	Flughund	Vrugterler-muis	—	—	Popo (all bats)	—	—	—	—	—	ibudibudi (bats all spp.)	—	—	—	—
Bat-eared Fox	Grossohrfuchs Löffelhund	—	—	—	—	pundugu	—	—	—	—	—	—	—	—	—
Genet-Cat	Ginsterkatze	Musk-Kat or Misselya-Kat	—	nsimba	kanu	nilili or nyilili	kanididi or kasimba	ndele	lunkwiri Kala	tandee	nghanu	—	kanu	kanu	—
Gerenuk or Waller's Gazelle	Giraffen-gazelle	—	E'nainját	—	mbuzi-twiga swala-twiga	—	—	—	—	—	—	Njera	—	—	—
Giraffe	Giraffe	Kameelperd or Giraf	Ol meút	indhlulamiti	twiga	nhwiga	twiga	tira	twia	tsámazo	mwhiga	ntigwa	twiga	nwiga	—
Grant's Gazelle	Grosse Gazelle	—	Ol Wargas	—	muhimbula	mbiza	kisi	—	muhimbula	gongosá	—	swala	—	—	—
Greater Kudu	Schrauben-antilope Grosser kudu	Koedoe	Ol maalo (H)	Ishongoyo or Ishongololo (Sh.)	tandala	nhandala	tandala, sikilo	nikio	sikilo	qokomi	sichilo	—	tandala	sikilo	—

Hare	Hase (var.)	Vlak, rooi and haas (diff. spp.)	—	Imvundhla	sungura	lung'wa-ndo or siyi	ka(w)u-ng'ando	mnya-ngaa	chunkula	lai	sungula	—		—	
Hartebeest—Coke's	Kuh-Antilope Kongoni-Antilope	Hartbees	Logwandi	—	kongoni	ng'oshi	konzi or ngonzi	—	kondi	gwarai	nyacibwinhu	nomgo-ni	—	—	—
„ Lelwel	—	—	—	—	kongoni	ng'oshi	konzi or ngonzi	—	—	—	—	—	—	—	—
„ Lichten-stein's	—	Moff-hart-bees or Kohlhart-bees	—	Nzanse (Sh.) or (Chi-ndao)	konzi or kongoni	—	—	—	—	—	nyacibwinhu	—	kongoni	—	—
Hedgehog	Igel	Krimpvarkie	—	Chitakatira	karu-nguyeye or uyaye	shilongo-mifa	karu-ngwiee or unguyeye	ke-nge	karu-ngwiee	kamase	sejesi	—	—	segesi	—
Hippopotamus	Nilpferd Flusspferd	Seekoei, nylperd, or rivierperd	Ol makau (H)	Imvubu	kiboko	ngubu or nguo	ntomo-mbo	tamondo	tara-mondo	maghu-ngo	nhomondo	vulu	tomo-ndo	tomo-ndo	njuba
Honey Badger	Honigdachs	Ratel	—	Indundu-ndwana or Inselo	nyegere	nyegele	siwuli, ki-buli or sambo	nyere	nyere	jiriba	muhiru	—	kikako	nyerge-ri	—
Hunting dog	Hyänenhund	Wildehond	osuyai (H)	Inkentshana	mbwaya mwitu, bizi	mhugi	ipuge	bugi	pugi	gweche	iminzi	—	potsho	miwi-nzi	—
Hyaena, Spotted	Gefleckte-Hyäne	Gesfikkelele-Hyaëna or Weerwolf	Ol ngójine	Impisi	fisi	mbiti	ipiti or kabiti-maluru	piiti	mpichi	tégele	iwelawela, mvisi	—	—	—	—
„ Striped	Gestreifte-Hyäne	—	—	Impisi	fisi and (?) ku-ngugua	italagu	papango-mbe or mbiti	piiti-mruri	kungu-gwa	condu	mvisilukunga	—	—	—	—
Hyrax	Klippschliefer	Dassie	—	Imbila	perere	mhimbi	kapimbi	pimbi	pimbi	cwena	mhimbi	—	mimbi	mimbi	—
Impala	Hochorn or Schwarz-fersen-anti-lope	Rooibok	En darokwe or Ol olo-lubo	Impala	para, Swala Nye-kundu	mhala	nswala or mpala	paa	támadi	xágado	mbata	—	nzimba	—	mpara
Jackal, Side-striped	Streifen-schakal.	jakkals	—	Impungucha	bweha	kidivi	likeye or limbwe	mura	monju	monjo	nhyewe	—	—	mchewi	—
„ Black-backed	Schrabacken-schakalo	Rooi-jakkals	—	—	—	—	—	—	—	—	—	—	—	—	—
Klipspringer	Klipp-springer	Klip-springer or Klip-bok	Engine (H)	Ingululu (Sh.)	nguru-nguru or mbu-zimawe	gulugulu	ngulu-ngulu	—	nguru-nguru	cecho	ngurunguru	—	kigu-nga	ngulu-ngulu	mpo-ndama-bare
Lemur	Ohrenmaki	Nagaappie	—	Impungutsha	komba	kamundi	kabundi	ndabi	danki	gabe	ndele or nha-ndalamiti	—	mwegi	mwegi	—
Leopard	Leopard	Luipard	Ol owaru Kéri (the spotted killer)	Ingwe	chui	subi or sui	subi or sui	ng'oi	sovi	tega	suwi	—	duma	duma	chui
Lesser Kudu	Kleine Kudu or Kleine Schrauben-antilope	Koedoe	O'sirám	—	kungu	—	tupala	—	sauda	tsauda	sawada	sulo	sawada	sawada	—

English	German	Afrikaans	Masai	Zulu and Shangan–Zulu	Kiswahili	Kisukuma	Kinyamwesi	Kinyaturu	Kirangi	Kisandawe	Chigogo	Kizigua	Kisagara	Kisungwa	Kn Bukoba
Lion	Löwe	Leeu (Lioness, Leeuwyfie)	Ol ngatun or Ol owáru **kiok** (the big killer)	Ingonyama or Imbuluweze or Imbudi	simba	shimba	simba	nyimba	simba	**xatsu**	simba	—	nyalupala	nyalupala	simba
Mongoose— " Common Banded	Mangu 1	Gebandemuishond	—	isidembo (Sh.)	ngutshiro	ng'hala	linkala or ikala	**kaara**	guchiro	**chwama**	**nghalasanga**	—	ngutchiro	Mchiro	mtshiro
" Large Grey	—	Kommetjiegat-Muishond or Kommetjiegat-Kat	—	—	—	—	—	—	—	—	—	—	—	—	—
" White-tailed	—	Witstert muishond	—	—	ngutshiro	karasa	—	—	—	—	nghungangome	—	—	—	—
" Black-tip-tail	—	Kleinvaal muishond	—	—	ngutshiro	—	—	—	—	—	mululumi	—	—	—	—
" Little	—	Dwerg muishond	—	—	ngutshiro	—	kamsio	—	—	—	muloli	—	**sindi**	**kimagala**	—
Mouse, Tree dor-	Mäuse	Boommuis	—	igundana	panya	—	—	—	—	—	tshimhanga	—	—	—	—
" Fat	—	Vetmuis	—	—	panya	—	—	—	—	—	funde	—	—	—	—
" Shamba	—	—	—	—	panya	—	liture	—	—	—	Mhanyalusanga	—	—	—	—
" Striped Grass	—	—	—	—	panya	—	—	—	—	—	**nyagalla**	—	—	—	—
" One-striped Grass	—	—	—	—	panya	—	—	—	—	—	fudi	—	—	—	—
" Gerbil	**Rennmaus**	—	—	—	panya panya	bewa	—	—	—	—	mbadya and mhanya	—	—	—	—
" Pigmy dor-	—	dwergmuis	—	—	panya	—	—	—	—	—	chipumbuza	—	—	—	—
Oribi	Bleichbock	Ourebi Owrebikje or Bleekbok	—	isiyamtai (Sh.)	taya kasia	mhundwi	pundunsya, pundwi, kasia	—	—	—	nhemanyika	—	—	—	nsilabo
Oryx	Beisa antilope or Spiessbock	Gemsbok or Gensbok	Ol kimāsarok	—	cheroa	—	—	—	—	Ol Kimaserok	**nyoganyoga**	**nchorocha**	—	—	—
Otters	Fisch-otter Weisswangenotter Krallenotter	**Kaapse otter** Gevlekte otter	—	—	fisi maji	—	nkonda	—	—	—	ndiamusu	—	**ififu**	**fwisi**	—
Pangolin	Schuppentier	Ystermagau	—	Itimi	kakakuona	ngakakuona nderabarya	kakakuona	**kugaga**	**kaka**	**kwarakaka**	nyamungumi	—	—	—	—
Pigmy Antelope or Suni	**Zwergbockchen Moschusbockchen**	**Pigmya**	—	Ihlengana (Livingstones)	paa	—	—	—	—	**goof**	—	—	—	—	—
Porcupine	**Stachelschwein**	**Ystervark**	—	Inungu	nungu(ri)	nunghu or huna	nunguri	**nungu**	**nungu**	**kiele**	**nungu**	—	—	—	—

Puku.	Gelbfussige-Moorantilope	Puku	—	—	—	—	—	—	—	—	—	—	—	—	—
Rats, Black	Hamsterratte	Swartrot	—	Igundana	panya	ngoso	koso, ngoso ikalayoyo	poku	—	buri	ngule	—	—	—	—
„ **Giant**	—	Reuserot	—	Magwinga (Sh.)	panya	—		—	—	—	nchesi	—	—	—	—
Reedbuck, Bohor	Riedbock	Rietbok	Erongo (H)	—	tohe	'nja	monge or injia	—	mbefi	kumpa	nhowi	ntohe	tohi	—	njasa
„ **Southern**	—	Reitbok	—	Inhlangu	—	—	—	—	—	—	—	—	—	—	—
„ **Chanler's Rock**	—	Rooi Rhebok	—	Inhlangwamatshe	—	—	—	—	—	—	—	—	—	—	—
Rhinoceros, black	Nashorn	Swart-renosteu	Emunye or Ol Schangito sabuk (the big fat beast —as for elephant)	Upejani	kifaru	mhela	para or pela	pembe	mpera	tsong	mhera	npera	mela	mela	nkura
Roan antelope	Pferdeantilope	Baster-eland	—	Mtagaisi	korongo	ng'horongo	korongo	—	—	bosi	—	nparahara	—	—	nkolongo
Rock-rabbit. See Hyrax															
Sable antelope	Rappenantilope	Swartwitpens	—	Impala-mpala	mpara, palahala or mbarapi	palahala	palapala or mpahala	—	—	—	—	nparahara	mparati	—	—
Serval Cat	Serval	Tierboskat	—	Indhlozi (Sh.)	mondo or kizonga	mondo	ibalabala	—	—	—	nzuli	—	—	—	—
Shrew	Spitzmaus	Spitmuis	—	—	kirukangia	kilamela	nhunga	—	—	—	nsunga	—	nyunga	nyunga	—
Situtunga	Sumpfbock; Wasserkudu	Waterskaap or Waterkudu	—	—	—	—	njobe	—	—	—	—	—	—	—	njobe
Spring-Hare	Springhase	Springhaas	—	—	kamendegere	huna	kasima	jiibu	tuju	dira	—	—	—	—	—
Squirrels	Eichhörnchen	Eekhoorntjie	—	Tshindana (Sh.)	Panya wa miti	—	—	—	—	—	chimweje and musila (ground)	—	—	—	—
Steinbucks	Steinantilope Steinböckchen	Steenbok, Vlaktebok or Bleekbok	—	Iqina	dondoro	sala	kazimba or mburunga	—	kerentula	ebla	chizimba	—	dondoro	—	—
Thomson's Gazelle	Zwerggazelle	—	éngoilin	—	lala	lala	lala	—	njera	sosonga	nzera	swala	—	—	—
Topi	Leierantilope	—	—	—	nyamera	ng'hiri	nyamera	—	—	—	—	—	—	—	ndagazi or nyamera
Vervet Monkey	Grune-Meerkatze or Kusten-Meerkatze	Aapie or Blannaap	—	Inkau.	tumbili or ngedere	nhumbiri	numbile or itumbili	tumbii	tumbili	qaku	njadengwa	—	ngedere	dodwa	—
Wart-hog	Warzenschwein	Vlakvark	—	Inhlovadawana	ngiri	ngiri	ngiri	ngiringii	ngiri	xaa(n)	njili or ngiri	—	ngiri	sikeloliwala	ngiri

English	German	Afrikaans	Masai	Zulu and Shangan-Zulu	Kiswahili	Kisukuma	Kinyamwesi	Kinyaturu	Kirangi	Kisandawe	Chigogo	Kizigua	Kisagara	Kisungwa	Kn Bukoba
Waterbuck, Defassa	Hirschantilope	Waterbok	—	Ipiva (Sh.)	kulo or kuru	—	ndoi	—	—	—	nghulo	nkuro	kaputa	ngoolo	nsama
„ Common	Gewohnlicher-Wasserbock or Ellipsen-Wasserbock	Waterbok or Kringgat	—	—	—	—	—	—	—	—	—	—	—	—	—
Weasels, Striped Lesser	Kappen-Iltis or Streifenwiesel	Slang Muishond	—	—	—	—	—	—	—	—	—	—	—	—	—
„ Greater (Zorilla)	Band-Iltis, or Zorilla	Stink or Oetrepte Muishond	—	—	Kisoke or Kanu	—	—	—	—	—	malulengwe	—	—	—	—
Wild Cat	Wilde Katze	Wildekat or Grauund-Kat	—	Impaka or Imbodhla	kimburu or paka wa pori	kimburu	kimburu or nyabuya-nvipari	kimburu	daalama	paka	mvugi or ivu-dye	—	kimbulu	kimbulu ?	—
Wildebeests—															
Blue or Brindled	Streifengnu or Blaugnu	Baster or Blouwildebees	O'engát	Inkonekone	nyumbu	mbushi	mbusi or mlusi	mbusi	kaatika	bus	nyumbu	nyumbu	nyumbu	—	—
„ White Bearded	Weissbartgnu	Witbaard-blouwildbees	—	—	—	—	—	—	—	—	—	—	—	—	—
Zebras	Bergpferd or Zebra	Sebra or Quagga	Ol oitigo (H)	Iduba	pundamilia	ndulu or ndolo	ndoru, ndulu or mbega	ndoo	njoe	doro	nhyenje	npudamilia	sangeri	sangeri	ntulege

Notes.—(i) " Swala " is used in many languages and with small variations for almost any small antelope. " Sara " does, however, appear to be the genuine name for the steinbuck in the Kisukuma language.

(ii) Corrections and additions to the native names are invited. Under " Kisandawe," clicks are represented by the conventional c, gq, q, and x used in writing the Zulu language. The gutteral is represented by gh, and the nasal vowel by (n) placed after the vowel letter.

(iii) In the native words generally the accent is usually on the penultimate syllable; otherwise the accented syllable is indicated by an accent thus: á.

(iv) In the consonants ng (written thus) the g is hard as in " tango "; when they are written ng' the g is soft as in " string."

APPENDIX 7.

A LIST OF PLANTS REFERRED TO IN THE PRESENT PAPER, WITH SOME NATIVE NAMES.

By B. D. Burtt, Botanist, Tsetse Research Department, Tanganyika Territory.

(Habitats revised by C. F. M. Swynnerton.)

The numbers refer to the vegetation communities so numbered in map 1, which should be referred to. Descriptive English names have been suggested where possible as an aid to memorization. Additions to the native names are invited. d.—dominant; co-d.—co-dominant; ch.—characteristic; l.—local; occ.—occasionally; a.—abundant; T.—Tanganyika territory.

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
1	*Abrus Schimperi* Hochst.	Papilionaceae.	Shrub.	Eluvial thicket in 7 and 9: 2 in Kondoa and Singida.	Central and Lake Prov.	ngagati	—	—	ko(ch)omia	—	—
2	*Acacia albida* Del.	Mimosaceae.	Large spreading tree.	Mainly riverine, esp. in 7, 8, and 9.	Widespread.	—	—	—	—	—	Large white-fruited acacia.
3	*Acacia Benthamii* Rochebr.	"	Small tree, mostly low-branching.	Eluvial, but commonly with underlying limonite crust. 7, 8, 9, but also, in places, 4.	Widespread.	ndubilo	—	—	muhinko	—	—
4	*Acacia Burttii* Bak. f.	"	Small, gall-acacia tree.	Hard-pan, in Kahama particularly.	Western Prov.	—	ulula	—	—	—	Large-leafed gall-acacia.
5	*Acacia campylacantha* Hochst.	"	Large tree.	Riverine, often overshading dense thicket, traversing most vegetational communities in T.T., incl. 1, 4, 7 and 9. Sometimes hill-sides under high rainfall.	Widespread.	(n)gu, mugu	mugu	—	mfa(ch)ancho	muwindi	Small-knobbed hook acacia.
6	*Acacia drepanolobium* Harms.	"	Thin, spindly gall-acacia tree, in old woods attaining some height and making fine building poles.	Hard-pan and other alluvial types, where d. Often pure stands.	Widespread.	ilula	ulula	—	mwandui	—	Common gall-acacia.
7	*Acacia Fischeri* Harms.	"	Small tree; sometimes covers ground densely for long distances as low shrubs.	Hard-pan, mainly in 7 and 9. Pure stands on limited areas.	Central and Lake Prov.	ihushi	katindiri	—	—	—	Ostrich-feather acacia.

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
8	*Acacia formicarum* Harms.	Mimosaceae.	Spindly, small gall-acacia tree.	Black alluvium, interspersed in most communities.	Central, Western and Lake Prov.	ilula	ulula	—	mwandui	—	Red-twigged gall-acacia.
9	*Acacia hebecladoides* Harms.	"	Medium tree.	Eluvial with *Combretum*, and semi-alluvial or alluvial as in Ankole, on Kuja and on Lambwe, with *Carissa-Rhus* thickets on ant-heaps. 3 in Bukoba.	Widespread.	—	ulula	—	—	mfunga-nyumba	—
10	*Acacia Kirkii* Oliv.	"	Low tree, with many stems radiating from base.	Alluvial flood plain anywhere but esp. in 7 and 9.	Central and W. Prov.	nsese	mnara	—	—	—	Green-barked or Pimple-pod ray-acacia.
11	*Acacia malacocephala* Harms.	"	Small tree, gall-acacia.	Hard-pan, in 7.	Northern and Lake Prov.	ilula	—	—	—	—	Downy-flowered gall-acacia.
12	*Acacia mellifera* Benth.	"	Small tree, or large shrub, bushy.	Hard-pan, esp. in 7 and 9.	Widespread.	ilugala	murugara	—	m(ch)ubwa	kisasa	Wait-a-bit acacia.
13	*Acacia nefasia* Schweinf.	"	Medium tree.	Riverine, incl. seasonal waters.	Widespread.	suhwa	msua	—	mkese	—	Large white-thorn acacia.
14	*Acacia orfota* Schweinf.	"	Shrub.	Alluvial flood plain.	Northern Prov.	—	—	—	—	—	—
15	*Acacia pallens* Rolf.	"	Tall tree.	Hard-pan, alluvial plains (extensive pure wooding) and, scattered, on hill-sides in 4.	Widespread.	mhama	mkambala	mkambala	m(ch)ubu	kambala	Large-knobbed hook acacia or "Knobby thorn."
16	*Acacia pennata* Willd.	"	Wide-rambling shrub.	Thickets, generally.	Widespread.	gege	—	—	—	lusewa	Bramble acacia.
17	*Acacia Rovumae* Oliv.	"	Large tree.	Hard-pan, and "fossil" alluvium.	Widespread.	mgongwa	mgongwa	—	—	—	Fluted umbrella-acacia.
18	*Acacia Seyal* Del.	"	Slender tree.	Alluvium.	Widespread.	ilulameru; masindi	mlela	—	muria	—	Yellow-barked gall-acacia.
19	*Acacia Senegal* Willd.	"	Small tree.	Mainly hard-pan, in 7, 8, 9.	Widespread.	ngwata	—	—	mjoji	kisasa	Sudan gum-acacia.
20	*Acacia spirocarpa* Hochst.	"	Large, flat-topped tree.	Under seemingly various edaphic conditions in 7, 8, 9; often on underlying limonite crust.	Widespread.	ngunga	mgunga	—	miwunga	mfunga-nyumbo	Corkscrew-fruited umbrella-acacia.
21	*Acacia Stuhlmannii* Taub.	"	Small tree, stems radiating.	Alluvial, flood plain, usually. Road-banks near Tanga.	Widespread.	nsese	mnaro	—	—	—	Hairy ray-acacia.
22	*Acacia usambarensis* Harms.	"	Large tree.	Hard-pan. Some other alluvial types; in 7, 8, 9 esp. and enclaves in 1 and 4—esp. in the east.	Widespread.	miriwa-nhwiga, ntulangoi	livindwe	—	—	mkongoi	Stink-bark acacia.

23	*Acacia xanthophloea* Benth.	Mimosaceae.	Very large tree.	Riverine.	Central and North Prov.	—	—	—	—	—	Yellow-barked fever tree.
24	*Acacia zanzibarica* Taub.	„	Small tree, gall-acacia.	Hard-pan.	Coastal.	—	—	—	—	—	Coastal gall-acacia.
25	*Acalypha ornata* Hochst.	Euphorbiaceae.	Dense shrub.	Thickets, esp. riverine, in 1, 4, 9, 7, esp. as interspersed in 1 in Kilosa–Handeni.	Widespread.	—	—	—	—	—	—
26	*Acanthus arboreus* Forsk.	Acanthaceae.	Shrub, not wide-branching, evergreen, thistle-like.	Thickets, in assocn. with high grass-jungle often on rain-forest outskirts.	Uganda, locally in Tanganyika (5).	—	—	—	—	—	Pink-flowered acanthus.
27	*Achyranthes aspera* L.	Amarantaceae.	Herb.	Riverine.	Widespread.	—	—	pangaza-wazuka	—	—	Splinter weed.
28	*Adansonia digitata* L.	Bombacaceae.	Huge tree.	On eluvial and in thickets, often on colluvial, in 7, 9, 8, 6, sometimes 4. Very prominent (d.) in cultivation steppe (*e.g.* in 13 in Lake Prov.), because unfelled.	Widespread.	ngwanda, mwandu	—	mbuyu	mwandu	mpera	Baobab tree.
29	*Adenia globosa* Engl.	Passifloraceae.	A succulent forming a large sphere above ground.	Hard-pan, in Masai-land.	Northern Prov.	—	—	—	—	—	Great spiny desert tuber.
30	*Aeschynomene elaphroxylon* Taub.	Papilionaceae.	Tall, open shrub.	Lake-shore, in marginal water.	Lake Victoria esp., other lakes large and small.	malindi	—	—	—	—	Ambatch.
31	*Afrormosia angolensis* Harms.	„	Medium largish tree.	D. or co-d. in much of 5 and in (S. Tabora) interzone in miombo between eluvial and hard-pan.	Widespread.	mwanga	mwanga, mubanga	—	—	—	White-barked post-wood.
32	*Afzelia quanzensis* Welw.	Caesalpiniaceae.	Very large tree.	In same interzone, also through thorn-bush (7) in eluvial thicket, or where otherwise initially sheltered from fires.	Widespread.	nkola	mkola	mbamba-kofi	m(ch)ola	mkonko	Lucky-bean tree or Pod Mahogany.
33	*Albizzia Antunesiana* Harms.	Mimosaceae.	Tallish tree, slender.	In miombo (*Brachystegia–Isoberlinia*) (v. p. 58). Ch.	Widespread.	—	—	—	—	—	Silver-lined albizzia.
34	*Albizzia brachycalyx* Oliv.	„	Small tree (mostly).	In thickets generally —commonly by stream-sides or over underground waters in 7, 8, 9.	Widespread.	shishiguru	—	—	msungua	—	Thicket albizzia.
35	*Albizzia glabrescens* Oliv.	„	Tree.	Riverine.	Eastern areas.	—	—	—	—	mkengo	Evergreen albizzia.
36	*Albizzia Harveyi* Fourn.	„	Medium tree.	Hard-pan and fossil mbuga and their margins in 7, 8, 9, and, as interspersals, elsewhere.	Widespread.	mpogoro	mpogoro	—	mpowo	mfirigisi	Short feather-leafed albizzia.

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
37	*Albizzia Lebbek* Benth.	Mimosaceae.	Medium tree.	Cultivated and as escape.	An escape chiefly in 6.	—	—	mkingu	—	—	Lebbek.
38	*Albizzia maranguensis* Taub. (staminal tube very short).	,,	Largish tree.	Rain forest or its outskirts.	Kilimanjaro.	—	—	—	—	—	Kilimanjaro albizzia.
39	*Albizzia gummifera* (Gmel.) Sm. (known formerly as *fastigiata* and *sassa*, staminal tube very long).	,,	Medium to large tree, umbrella top.	Rain forest, usually marginal only for full rain forest, but as co-d. with *Panax* in temperate forests on Kaguru Mts. N. of Kilosa and in ravine-type forest.	Widespread.	—	—	—	—	mkengo	Forest flat-topped albizzia.
40	*Albizzia chirindensis* Swynnerton.	,,	Slender tree, many storeyed.	Rain forest outskirts.	S. Rhodesia.	—	—	—	—	—	Black-barked storeyed albizzia.
41	*Albizzia sericocephala* Benth.	,,	Medium tree, spreading.	Hard-pan and "fossil" mbuga, chiefly in 7, 9, 8.	Widespread.	mpogoro bongore	mpogoro	—	mpowo	mfirigisi	Ostrich-feather albizzia.
42	*Albizzia tanganyikensis* Bak. f.	,,	Medium tree.	1, miombo (*Brachystegia–Isoberlinia*).	Central and West Prov.	—	—	—	—	—	Paper-bark albizzia.
42a	*Albizzia versicolor.*	,,	Medium tree.	Ditto, ch.	Widespread.	—	—	—	—	—	—
43	*Albizzia Zygia* Macbr.	,,	Tallish tree.	Rain forest, often secondary, and rain forest outskirts.	Lake Victoria.	—	—	—	—	—	—
44	*Ahlcornea cordifolia* Mull.	Euphorbiaceae.	Large shrub, sprawling branches.	Lacustrine secondary rain forest and lake beaches.	Lake Victoria.	—	—	—	—	—	Olunzibaziba (from the Luganda word).
45	*Allanblackia Stuhlmannii* Engl.	Guttiferae.	Very tall, straight tree.	Rain forest.	Usambara and Nguru Mts.	—	—	—	—	—	—
46	*Allophyllus griseotomentosus* Gilg.	Sapindaceae.	Shrub.	Thickets.	Widespread.	—	—	—	—	msemeleke	—
47	*Aloë* spp.	Liliaceae.	Succulent.	Desert hard-pan, dry thicket and rocks.	Widespread.	mpirimishi	—	—	—	—	Aloe.
48	*Anisophyllea obtusifolia* Engler and Brehmer.	Rhizophoraceae.	Small tree.	Rain forest and lake shore.	Usambara Mts., Islands, L. Victoria.	—	—	—	—	—	—
49	*Anona senegalensis* Pers.	Anonaceae.	Large shrub, spreading.	Eluvial, esp. in miombo country, in tree *Combretum* enclaves, 6 in grass-jungle (good rainfall) and (P.E.A.) on limestone; incl. 6, 4 and 1.	Widespread.	—	mtela	mtopetope mwitu	—	—	Wild custard-apple.
50	*Antiaris usambarensis* Engl.	Moraceae.	Tall tree.	Rain forest.	Eastern area—6 and back of it.	—	—	—	—	—	Mock mvule.
51	*Anthocleista orientalis* Gilg.	Loganiaceae.	Tall tree.	Ravine forest, secondary rain forest, incl. lacustrine, and rain forest outskirts.	Incl. Usambara Mts. and (*orientalis*?) L. Victoria.	—	—		—	—	Giant-leaf tree.

52	***Asparagus Pauli-guilielmi*** Sol.	Liliaceae.	Woody climber.	Eluvial, with the erect Combretums.	Widespread.	kasolanka-nga msauwi	—	mwinoka-ngulu	—	—	—
53	***Aspilia*** sp.	Compositae.	Tall herb.	Black alluvium.	Widespread.	—	—	—	—	—	Tall yellow swamp daisy.
54	***Balanites aegyptiaca*** Del.	Zygophylla-ceae.	Medium tree, evergreen.	Hard-pan, lava-plain and some alluvial types.	Widespread.	nyuguyu	mwamba-ngoma	—	mudu-rchuu	mkonga	Bilharzia tree.
55	***Bambusa vulgaris*** Schrad. Mexico.	Gramineae.	Bamboo.	Cultivated.	—	—	—	—	—	—	Common bamboo.
56	***Baphia Burttii*** Bak. f.	Papilionaceae.	Large, coppicing shrub.	12, central group on map, Itigi thicket.	Central Prov.; a *Baphia* in Buhungu-kira, Lake Prov.	—	muhingiri	—	—	—	—
57	***Baphia massaiensis*** Taub.	"	Large, coppicing shrub.	12. Central group, Itigi thicket.	Central Prov.	—	muhingiri	—	mwehi-ngiri	—	—
58	***Borassus flabellifer*** var. ***aethiopica*** Warb.	Palmae.	Tall palm tree, bulge in stem.	Riverine in 7 and 9, also scattered singly or in groves under fair rainfall or near water by elephants and man—in 1 and 11 (l.).	Widespread.	—	muhama	—	mpama	mkwaba	Borassus palm.
59	***Bauhinia Thonningii*** Schum.	Caesalpini-aceae.	Small to medium tree.	Alluvial and semi-alluvial.	Widespread.	ntinda-mbogo	mfundwa-mbogo	msegese	—	—	Calf's-foot.
60	***Berlinia Scheffleri*** Harms.	"	Tall tree.	Rain forest.	Usambara Mts.	—	—	—	—	—	—
61	***Bersama*** spp.	Melianth-aceae.	Medium to large trees.	Rain forest.	Widespread.	—	—	—	—	—	—
62	***Bidens*** spp.	Compositae.	Herbs.	Weeds of cultivation (13) and (l.) 7 and 9.	Widespread.	—	—	—	—	—	Black-jack.
63	***Brachylaena Hutch-insii*** Hutch.	"	Tall tree with persistent axis.	Closed plateau forest, v. definition.	Tanga Prov. Kikuyu.	—	—	—	—	—	Tall silver-leaf.
64	***Brachystegia flagristi-pulata*** Taub.	Caesalpini-aceae.	Medium tree.	1, miombo (*Brachy-stegia–Isoberlinia*). l.d.	Eastern and Lake Prov.	—	mienzi	miombo	—	—	Ostrich-feather miombo.
65	***Brachystegia*** aff. ***ap-pendiculata*** Benth., Hutch. and Burtt Davy.	"	Small to tall slender tree.	1 and 2, miombo (*Brachystegia–Iso-berlinia*), often d. and co-d.	Widespread.	ntundu	mtundu (wanga-ka)	miombo	—	—	Smooth-leafed common miombo.
66	***Brachystegia itoliensis*** Taub.	"	Same.	1 and 2, miombo (*Brachystegia–Iso-berlinia*), often d. and co-d.	Widespread.	ntundu	mtundu (molo)	miombo	mupumbu	mbonha	Downy-leafed com-mon miombo.
67	***Brachystegia micro-phylla*** Harms.	"	Large tree, spreading, cedar-like top.	High hills, scarps and rock outcrops in 1, l. d.	Widespread.	—	mgara	—	mkinki	mdanda-ranyani	Mountain miombo.
68	***Brachystegia wanger-meeana*** de Willd. (South Tabora).	"	Small tree.	1, miombo (*Brachy-stegia–Isoberlinia*).	Western Prov.	—	kashishi	—	—	—	Small flat-top mi-ombo.
69	***Brachystegia glaber-rima*** R. E. Fries. (South Tabora).	"	Largish tree.	1, miombo (*Brachy-stegia–Isoberlinia*).	Western Prov.	—	mshilanga	—	—	—	Blue under-leaf miombo

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
70	*Bridelia micrantha* Baill.	Euphorbiaceae.	Medium tree.	Riverine, rain forest outskirts and high-rainfall grass-jungle.	Widespread.	—	—	—	—	—	Black-berried yoke-wood.
71	*Burkea africana* Hook.	Mimosaceae.	Tallish, slender tree.	1, miombo (*Brachystegia–Isoberlinia*); ch., occ. d. (Bechuanaland (l.).	Widespread.	—	mgando	—	—	—	Burkea red-wood.
72	*Burttia prunoides* Bak. f. and Exell.	Connaraceae.	Small bushy tree or large shrub.	12, Central group, Itigi thicket, l. co-d.	Central and Lake Prov.	—	—	—	—	—	Thicket cherry-bloom.
73	*Bussea massaiensis* Harms.	Caesalpiniaceae.	Small tree.	12, Central group, Itigi thicket, l. co-d.	Central Prov.	—	msape	—	mnangana	—	Gold-flowered iron-wood.
74	*Callitris robusta* R.Br. Australia	Coniferae.	Tallish tree, persistent axis, long-persisting lower branches.	Cultivated.	[N.S.W. and S. Australia.]	—	—	—	—	—	"Australian pine" or desert sandarac.
75	*Cananga odorata* Hook. f.	Anonaceae.	Medium tree.	Cultivated at Amani.	[Burma and Malaya.]	—	—	—	—	—	Ilangilang.
76	*Canarium Schweinfurthii* Engl.	Burseraceae.	Large tree	—	[Trop. Afr.]	—	—	—	—	—	African elemi.
77	*Canthium* spp.	Rubiaceae.	Small trees, shrubs or trailers.	Thickets and closed-forest outskirts.	Widespread.	—	mnindi	—	—	—	Lion's lair (translation of its Shangan-Zulu name).
78	*Carissa edulis* Vahl.	Apocynaceae.	Shrub, trailing, sometimes climbing, evergreen.	Hard-pan thicket in Masailand, riverine and ant-heap thicket elsewhere.	Widespread.	—	—	mkalalime	—	—	Common black-berried carissa.
79	*Cassia abbreviata* Oliv.	Caesalpiniaceae.	Small tree.	Hard-pan and equivalents.	Widespread.	mrunda-runda	munzoka	—	mpapati	mkunde-kunde	—
80	*Cassia didymobotrya* Fresen.	,,	Large, bushy shrub, strongly musk-smelling.	Alluvial flood plain, sandy river deposits.	Widespread.	—	—	—	—	—	Musk-scented cassia.
81	*Cassia siamea* Lam.	,,	Largish tree, nearly evergreen.	Cultivated: succeeds nearly everywhere from rain-forest neighbourhood to 7.	Widespread under cultivation. [India and Malaya.]	—	—	—	—	—	Siamese cassia or Malayan iron-wood.
82	*Cassipourea mollis* (Fries) Alston.	Rhizophoraceae.	Small tree.	12, Central group on map, Itigi thicket, Coast thicket (l.).	Chiefly Central and West Tanganyika.	—	—	—	—	—	—
83	*Castilloa elastica* Cerv.	Moraceae.	Tree.	Cultivated at Amani.	Central America.	—	—	—	—	—	Mexican rubber.
84	*Cedrela mexicana* M. Roem. Central America.	Meliaceae.	Tall, straight tree.	Cultivated at Amani.	—	—	—	—	—	—	Mexican cigar-box-tree.
85	*Cedrela odorata* L. S. America.	,,	Large tree.	Cultivated at Amani.	[S. America.]	—	—	—	—	—	Cigar-box-tree or "bastard cedar."
86	*Celtis Durantii* Engl.	Ulmaceae.	Large tree.	Rain forest.	Widespread.	—	—	—	—	—	Stenchwood.
87	*Chlorophora excelsa* Benth.	Moraceae.	Very large tree.	Rain forest and as cultivation-weed, 13 back of Tanga.	Eastern areas back to Kilosa; and Uganda.	—	—	mvule	—	muhurli	Mvule.

88	*Chrysophyllum natalense* Sond.	Sapotaceae.	Small to medium tree, evergreen.	Ravine forest and secondary rain forest.	Widespread.	—	—	—	—	—	—
89	*Cissus quadrangularis* L.	Ampelidaceae.	Succulent climber.	Deciduous thickets in 7, 9, 8.	Widespread.	—	—	—	—	kurubuka	Ribbed-stem vine.
90	*Cissus rotundifolia* Engl.	,,	Succulent climber.	Deciduous thickets, same.	Widespread.	—	—	—	—	kurubuka	Fleshy-leafed vine.
91	*Clausena anisata* Oliv.	Rutaceae.	Large shrub.	Plateau forest. In rain forest (usually secondary), scarcer.	Widespread.	—	—	—	—	—	Absinthe bush.
92	*Cocos mucifera* L.	Palmae.	Palm tree.	Cultivated widely.	Coastal. [Reg. Trop.]	—	—	nazi	—	—	Coconut palm.
93	*Coffea arabica* L.	Rubiaceae.	Large shrub or small tree, evergreen.	Cultivated in good-rainfall hill areas.	Cultivated:—Amani to Arusha, Mt. Oldeani, Bukoba, Iringa-Mbaya highlands, Kenya, Uganda, Nyasa, and Abercorn in N. Rhodesia. [Arabia.]	—	—	buni	—	—	Arabian coffee.
94	*Coffea robusta* L. Linden.	,,	Same.	Cultivated.	Cultivated Bukoba and Amani. [Belgian Congo.]	—	—	buni	—	—	Robusta coffee.
95	*Combretum apiculatum* Sond.	Combretaceae.	Small tree, erect growth.	Eluvium in miombo, colluvium interzone and a form of hard-pan alluvium (v. pp. 67–68 and app. 4).	Widespread.	—	msana-tembo	—	mlahie mdogo	—	Small-fruited common tree-combretum.
96*a*	*Combretum Fischeri* Engl.	,,	Small tree.	Common in miombo. Sometimes in hard-pan.	Widespread.	—	mlandala	—	—	—	Pale-underleafed scaly combretum.
96*b*	*Combretum longispicatum* Engl.	,,	Trailing shrub or woody climber.	Eluvial thickets in 7 and 9.	Lake Prov. and fairly widespread.	—	—	—	—	—	Pink tooth-brush combretum climber.
97	*Combretum molle* R. Br.	,,	Small tree.	Rocky hills.	Lake Prov.	—	—	—	—	—	—
98	*Combretum obovatum* F. Hoffm.	,,	Large woody climber.	Riverine and eluvial thicket.	Widespread.	goweko	mgoweko (mkubwa)	—	mrombo-rombo	—	White-leafed combretum climber.
99	*Combretum padoides* Engl.	,,	Large woody climber.	Riverine.	Eastern areas.	—	—	—	—	—	May-blossom combretum.
100	*Combretum parvifolium* Engl.	,,	Coppicing shrub.	Hard-pan thicket, d.	Central and Western areas.	lowashi	—	—	moria-ndata	—	Hard-pan thicket combretum.
101	*Combretum purpureiflorum* Engl.	,,	Large woody climber.	Hard-pan, limey and limonite.	Central and Western areas.	goweko	mgoweko (mdogo)	—	—	—	Scarlet tooth-brush combretum climber.
102	*Combretum splendens* Engl.	,,	Small tree.	Eluvial generally incl. 1, 7 and 9, and a form of hard-pan alluvium (v. p. 67).	Widespread.	nama	mlama	—	—	—	Net-barked, woolly-leaf combretum.

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
103	*Combretum ternifolium* Engl.	Combretaceae.	Small tree.	Hard-pan and other alluvium, both as glade and "mbuga." Most closely associated with 1, miombo. On hillsides in Musoma.	Widespread.	mujaminzi	mujaminzi, muluja	—	—	mlama	Glossy-leafed glade tree-combretum.
104	*Combretum trichopetalum* Engl.	,,	Large woody climber.	Riverine and eluvial thickets.	Central, Lake and Western Prov., T.	lhegelya	isantulya-ngoko	—	—	—	Strong-veined combretum climber.
105	*Combretum Trothae* Engl. & Diels.	,,	Small tree or coppicing shrub.	12. Central group on map, Itigi thicket.	Central Prov.	—	mnagana	—	mnangana	—	Itigi-thicket tree-combretum.
106	*Combretum Zeyheri* Sond.	,,	Small tree, l. fairly large (as near Kilosa).	Eluvial (common in 1 and 2, miombo), colluvial, and forms of hard-pan alluvial.	Widespread.	msana	msana	—	mlahie kubwa	—	Large-fruited common tree-combretum.
107	*Commiphora Fischeri* Engl.	Burseraceae.	Small tree, orchard-tree form.	Eluvial, in "thorn-bush" (7 and 9), co-d. with *Ostryoderris* (189, below) and *C. ugogensis* (113). Small enclaves in 1, miombo, esp. forming rings on and round ant-heaps.	Central and Western Tanganyika.	ndonho, apunzanhe	mtonto	—	mtoto	—	Large-leafed trifoliate commiphora.
108	*Commiphora pilosa* Engl.	,,	Small tree, orchard form.	Eluvial, often with erect combretums preceding. Common also in 8.	Widespread.	mhagashi	mponda	—	mlaha	mtiwinhi	Downy-leafed green-barked commiphora.
109	*Commiphora Schimperi* Engl.	,,	Small tree, orchard form.	Hard-pan, co-d. with *Lannea humilis*. Mainly in 7, 9, 8.	Central and Western Tanganyika esp.	mponda	—	—	—	—	Resin-scented green-barked commiphora.
110	*Commiphora Scheffleri* Engl.	,,	Small tree.	Hard-pan, Masailand, 9.	Northern Prov.	—	—	—	—	—	—
111	*Commiphora subsessilifolia* Engl.	,,	Small tree, orchard-tree form.	Riverine, sometimes hard-pan. 7 and 9.	Central and Western Tanganyika esp.	lueja	mponda	—	—	—	Scentless green-barked commiphora.
112	*Commiphora Stuhlmannii* Engl.	,,	Small to medium tree, splayed branches.	Thickets generally.	Central and Western Tanganyika esp.	nkungulu	mponda	—	mutar-rumbu	—	Ant-hill commiphora.
113	*Commiphora ugogensis* Engl.	,,	Medium to largish tree.	Co-d. sometimes in eluvial savanna, 7 and 9. Tree-d. in eluvial thickets in the same.	Central and Western Tanganyika esp.	nsusu	—	—	msaki	—	Large yellow-barked commiphora.
114	*Coleus igniarius* Schweinf.	Labiatae.	Succulent shrub.	Semi-desert.	Central and North Prov.	—	—	—	—	—	Desert-lavender coleus.

115	*Copaifera mopane* Kirk.	Caesalpinieae.	Large tree.	Alluvial and semi-alluvial.	[The Rhodesias and Nyasaland.]	—	—	—	—	—	Mopane.
116	*Cordyla africana* Leur.	Papilionaceae.	Tree.	Deciduous thicket.	Eastern Prov., T.T.	—	—	—	—	—	—
117	*Costus subliflorus* K. Schum.	Zingiberaceae.	Fleshy-stemmed sprawling shrub.	Rain forest, esp. "lowland" and secondary rain forest.	Usambara Mts.	—	—	—	—	—	—
118	*Craibia Burttii* Bak. f.	Papilionaceae.	Smallish, erect-standing tree, evergreen.	12, Central group, Itigi thicket.	Central Prov.	—	—	—	—	—	Burtt's craibia.
119	*Crossopteryx febrifuga* Benth.	Rubiaceae.	Small tree.	Eluvial and colluvial, with the erect Combretums.	Widespread.	—	msamza-mbeki	—	—	—	—
120	*Cupressus arizonica* Greene.	Cupressaceae.	Tall tree, conifer form.	Cultivated. [Arizona.]	—	—	—	—	—	—	Arizona cypress.
121	*Cussonia Zimmermannii* Harms.	Araliaceae.	Medium, thick stubby twigs, little branching.	—	Usambara Mts.	—	—	—	—	—	Usambara cussonia.
122	*Dalbergia melanoxylon* G. et P.	Papilionaceae.	Small tree.	Hard-pan and semi-alluvial types, 6 (l.), and 7. Occ. interspersal in 1.	Widespread.	ngembe	mgembe	mpingo	mpako	mhingo	Pod ebony.
123	*Dalbergia Stuhlmannii* Taub.	„	Small tree.	Eluvial or colluvial, with the erect Combretums.	Widespread.	mfifi	mfifi	—	—	mzeza	—
124	*Dichrostachys glomerata* Hutch. & Daly.	Mimosaceae.	Shrub to small tree.	Hard-pan, esp. in mbuga-edges in 9 and 7.	Widespread.	nhundulu	mtundulu	mtula jambe	ntundu	chikule-gembo	Tassel-flower thorn.
125	*Diplorhynchus mossambicensis* Benth.	Apocynaceae.	Small to medium tree, weeping.	1, Miombo (*Brachystegia–Isoberlinia*). Ch. of some sub-types.	Widespread.	msongati	msonga	—	—	mtogo	Weeping diplorhynchus.
126	*Disperma quadrisepalum* Clarke.	Acanthaceae.	Shrub.	Riverine thickets.	Central and N. Prov.	—	—	—	—	—	—
127	*Dombeya reticulata* Mast.	Sterculiaceae.	Small tree.	Eluvial, with *Combretum*.	Widespread.	—	—	—	—	—	—
128	*Dombeya rotundifolia* Harv.	„	Small tree.	Eluvial hill-sides or colluvium, often with the erect Combretums. Gregarious.	Widespread.	—	—	—	—	mswayu	Cherry blossom Dombeya.
129	*Ekebergia Meyeri* Engl.	Meliaceae.	Large tree.	Rain forest, mainly outskirts. Closed forest Arusha.	S. Rhodesia and Mount Meru.	—	—	—	—	—	—
130	*Entada abyssinica* Staud.	Mimosaceae.	Small tree or large shrub.	Eluvial and colluvial, often with erect Combretums.	Widespread.	—	—	—	—	—	—
131	*Erythrina Burttii* Bak. f.	Papilionaceae.	Large and striking, umbrella form tree.	Hard-pan, Masailand, 9.	Central and N. Prov.	—	—	—	—	—	Small-leafed umbrella erythrina.
132	*Erythrina tomentosa* R. Br.	„	Tree, small to medium.	Eluvial: grass and tree savanna on hill-sides, granite and other, incl. (*e.g.*) Kilimanjaro. Grass-jungle (*e.g.* Uganda).	Widespread.	nsala-nhunda	mhalalwa-huba	mlungu-magoma	—	—	Common rough-barked Kaffir-boom.

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
133	***Euphorbia bilocularis*** **N.E. Br.**	Euphorbiaceae.	Largish succulent tree.	Thickets and termite mounds, l.a. in most main communities, esp. 7, 9, 8 and 6.	Widespread.	langali	mlangali	—	mwongare	mlangali	**Greater euphorbia.**
134	***Euphorbia matabelense*** **Pax.**	„	Very angular little-foliaged shrub.	Hard-pan in 7 and 9 (S. Shinyanga, *e.g.*), and dry sites in miombo (*e.g.* S. Umtali, S. Rhodesia).	Widespread.	mulembosi	mulembosi	—	mtupetupa	lugovu	Bird-lime euphorbia.
135	***Euphorbia Tirucalli*** L.	„	Succulent large shrub or small tree, dense, evergreen.	Xerophyte thickets (as in Sonyo), dry rock outcrops (as in Zululand).	Widespread as native hedge-plant.	nala	—	manyara	mpipiti	—	Manyara.
136	***Fagara chalybaea*** **Engl.**	Rutaceae.	Small tree.	Thickets in hard-pan (esp. 7 and 9).	North and Central Prov.	—	—	—	—	—	—
137	***Fagara Merkeri*** **Engl.**	„	Small tree.	On eluvial soil, commonly.	Widespread.	nungu, mrungurungu	mdalu	—	mulungu	mkunungu	Knobby barked hooked-thorn fagara.
138	***Faurea saligna*** **Harv.**	Proteaceae.	Medium tree, sawable.	Upland eluvial.	—	—	—	—	—	—	Boeken-hout (S. A. Dutch).
139	***Faurea speciosa*** **Welw.**	„	Small tree.	Upland eluvial, with *Protea*, *Parinarium*, *Sizygium owariense*, etc. Sometimes co-d.	Widespread.	—	—	—	—	—	Woolly boeken-hout.
140	***Ficus exasperata*** **Vahl.**	Moraceae.	Shrub or tree.	Riverine and closed forest.	Widespread.	—	—	—	—	—	Sand-paper fig.
141	***Ficus Sycomorus*** **L.**	„	Large tree.	Riverine.	Widespread.	mkuyu	—	mkuyu	mkuyu	mkuyu	Common wild fig.
142	***Flueggia*** **sp.**	Euphorbiaceae.	Large shrub.	Riverine and rain-forest margin.	Widespread.	—	—	—	—	—	—
143	***Funtumia elastica*** **Stapf.**	Apocynaceae.	Tree.	Cultivated.	At Amani. [Trop. Afr.]	—	—	—	—	—	—
144	*Garcinia Livingstonii* T. Anders.	Guttiferae.	Large tree, evergreen.	Riverine forest.	Widespread.	—	kanula	—	—	—	—
145	***Gigantochloa ater*** **Kurz.**	Gramineae.	Huge bamboo.	Cultivated.	At Amani. [Java.]	—	—	—	—	—	Great bamboo.
146	***Grevillea robusta*** **A. Cunn.**	Proteaceae.	Large tree.	Cultivated—widely, as shade for Coffee, see under 93, above.	Chiefly Northern and Tanga Provinces. [N.S.W. and E. Australia.]	—	—	—	—	—	" Silky oak."
147	*Grewia bicolor* Juss.	Tiliaceae.	Coppicing, branch-spreading shrub.	Thickets very generally.	Widespread.	nkoma	mkomalende	—	mpenehe	mkore	White under-leafed grewia.
148	*Grewia Burttii* Exel.	„	Coppicing, branch-spreading shrub.	Area 12, Central group on map, Itigi thicket.	Central and Lake Prov.	—	—	—	memsa-mpemehe	—	Itigi-thicket grewia.
149	*Grewia similis* K. Schm.	„	Coppicing, branch-spreading shrub.	Hard-pan thicket (*e.g.* in 7 and 9).	Widespread.	mdagwasa	—	—	—	—	Pale green grewia.

150	*Grewia villosa* Juss.	Tiliaceae.	Coppicing, branch-spreading shrub.	Hard-pan do., Masai-land, 9.	N. Prov.	—	—	—	—	—	Hairy desert grewia.
151	*Gymnosporia* sp.	Celastraceae.	Small tree.	Mainly hard-pan and equivalents.	Widespread.	—	mwegya	—	—	mwamba-ngoma	—
152	*Haronga madagascariensis* Lam.	Guttiferae.	Tree, small to medium.	Rain-forest outskirts. A pioneer invader thence of savanna on stoppage of burning.	Widespread.	—	—	mkuntu	—	—	—
153	*Harrisonia abyssinica* Oliv.	Simarubaceae.	Shrub with trailing bramble-like branches.	Riverside savanna, colluvial and alluvial edges of glades and mbugas and an interzone plant in the better-grassed miombo; 1 (esp. in East), 9 and 7.	Widespread.	datula, nsomanjala	—	mkunzu	—	mkunzu	Harrisonia bramble.
154	*Hibiscus cannabinus* L.	Malvaceae.	Tall herb.	Various communities.	Widespread.	ilaba	—	—	—	—	Tall purple hibiscus.
155	*Hoslundia opposita* Vahl.	Labiatae.	Broad, herbaceous-twigged shrub, small orange, edible berries.	Thicket-edges esp. under fair rainfall as in 1, 3, 4, 5, 6 and in grass-savanna in rain-forest areas.	Widespread.	—	—	mtere-mtere	—	—	—
156	*Hyphaene thebaica* Mart.	Palmae.	Palm tree.	—	Coastal.	—	—	—	—	—	Doum palm.
157	*Hyphaene coriacea* Gaertn.	Palmae.	Palm tree.	Alluvium, 9 and as enclaves in 1.	Central and Western areas of T.T.	mlala	—	—	—	—	Feather palm.
158	*Indigofera gyrocarpa* Bak. f.	Papilionaceae.	Tall woody shrub.	1, miombo, eluvial and amongst the trees themselves.	Central Prov.	—	—	—	—	—	—
159	*Ipomoea* spp. (many).	Convolvulaceae.	Profusely climbing herbs.	Most communities but esp. 9 and 7.	Widespread.	—	—	—	—	—	Savanna convolvulus.
160	*Isoberlinia globiflora* Hutch.	Caesalpiniaceae.	Small to tallish, slender tree.	1 and 2, miombo (*Brachystegia–Isoberlinia*), commonly (not always) as the dominant.	Widespread.	ntundu	muwa	—	murevea	mbonha	—
161	*Jasminum* spp.	Oleaceae.	Woody climbers.	Riverine thickets in 9, 7; coastal and other more humid thickets away from water.	Widespread.	—	—	—	—	—	Jasmine.
162	*Kalanchoë glandulosa* Hochst.	Crassulaceae.	Herb.	Semi-desert conditions, whether climatic or edaphic.	Widespread.	—	—	—	—	—	—
163	*Kickxia africana* Benth.	Apocynaceae.	Tree.	Cultivated at Amani.	—	—	—	—	—	—	—
164	*Kigelia aethiopica* Engl.	Bignoniaceae.	Largish tree.	Riverine in drier areas (7, 9); alluvium or colluvium in better-rain areas, as in enclaves in 1 in the East.	Widespread.	mwicha, ninji	mwiegea	mnyegea	mungungu	myagaya	German-sausage tree.

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
165	***Khaya nyasica*** Stapf. (? also ***senegalensis*** Guill. & Perr.).	Meliaceae.	Very large tree.	Heavy riverine and rain forest.	Mostly Eastern.	—	—	—	—	mkangazi	Eastern red African mahogany.
166	***Landolphia florida*** Benth.	Apocynaceae.	Huge woody climber.	Gallery forest, rain-forest outskirts and openings.	Widespread.	—	—	mbungo	—	—	Large-flowered Landolphia.
167	***Landolphia Kirkii*** Dyer.	„	Large woody climber.	Ravine forest and riverine. This or the next (*q.v.*) in 1. miombo, in S. Tabora.	Widespread.	—	—	mkilu-ngwana	—	—	Kirk's rubber vine.
168	***Landolphia petersiana*** Dyer.	Apocynaceae.	Large woody climber.	Riverine; this or *L. Kirkii* common in *Isoberlinia–Brachystegia* areas in Tanga and Western Provs.	—	—	mwugngo-ungwa.	mtoria	—	—	Peters' rubber vine.
169	***Lannea humilis*** Oliv.	Anacardiaceae.	Small tree.	Hard-pan in 7 and 9, co-d. with *Commiphora Schimperi*.	Widespread.	ntinje	mtinji	—	mwainti	—	Hard-pan lannea.
170	***Lannea fulva*** Engl.	„	Large shrub spreading branches.	Eluvial, and eluvial with laterite, incl. thickets, in 7 and 9.	Widespread.	nselya	mselya	—	—	—	Russet-leafed lannea.
171	***Lannea Kirkii*** Burtt-Davy.	„	Tree.	Hard-pan and riverine.	Widespread.	nsayu	—	—	—	mumbu	—
172	***Lannea Schimperi*** Hochst.	„	Fairly large tree.	Eluvial, in 7, 9, 4.	Widespread.	mumba, ngumba	mgumbu	—	—	mbure-zegwe	Greater lannea.
173	***Lantana salvifolia*** Jacq.	Verbenaceae.	Soft-wooded shrub.	Eluvial, with erect Combretums, upland savanna communities.	Widespread.	—	—	—	—	—	—
174	***Leonotis pepetaefolia*** R. Br.	Labiatae.	Tall herb, gregarious.	Alluvial flood plain.	Widespread.	—	—	—	—	—	Hollow-stock
175	***Lonchocarpus Capassa*** Rolfe.	Papilionaceae.	Tree, medium size.	Riverine in 7 and 9; and (see 206 below) interzone in miombo (1), with *Pteleopsis*, *Combretum*, etc.	Widespread.	male, mbale	mwale-wale	—	m(ch)ank (ch)oi	—	—
176	***Maba abyssinica*** Hiern.	Ebenaceae.	Tree, evergreen.	Granite hill-top thickets and rocks; thus fire-protected.	Widespread.	—	—	—	—	—	—
177	***Maesa lanceolata*** Forsk.	Myrsinaceae.	Large shrub (usually) or small tree, evergreen.	Rain forest outskirts, ravines, thickets in grass-jungle under good rainfall.	Widespread.	—	—	—	—	—	—
178	***Maerua crassifolia*** Forsk.	Capparidaceae.	Small tree.	Hard-pan, 9.	Central area of T.	—	kaninegwi	—	—	—	—
179	***Mangifera indica*** L.	Anacardiaceae.	Large tree, evergreen.	Cultivated, less successfully in 9 and 7 than in 1, 4 and 6.	Widespread.	nyembe	—	nwembe	—	—	Mango.

180	*Manihot Glaziovii* Muell.	Euphorbiaceae.	Smallish tree.	Formerly cultivated, now dominating a form of dense thicket.	Great plantations by the Germans in 6, 4, easterly 1, 3 and 8, and 13 back of Tanga. [Brazil.]	—	—	mpila	—	—	Ceara-rubber.
181	*Markhamia acuminata* K. Schm.	Bignoniaceae.	Tall shrub.	Eluvial thickets in 7 and 9 particularly, l. with erect Combretums in 1.	Widespread.	mubinza-uigutile	—	—	muwanda	mtala-wanda	Brown-flowered thicket markhamia.
182	*Markhamia obtusifolia* Sprague.	„	Tall shrub or small tree.	Eluvial in 9, 7; common with erect Combretums in 1.	Widespread.	mpapa	mbapa	—	mlili	mlanda-lukoa	Yellow-flowered felty markhamia.
183	*Markhamia platycalyx* Sprague.	„	Smallish tree (larger than 181, 182).	Lacustrine rain forest and ravine forest.	Uganda, Bukoba, Biharamulo, Ukara, etc.	—	—	—	—	—	Uganda markhamia.
184	*Microchloa indica* P. Beauv.	Gramineae.	Diminutive, sparse grass.	Hard-pan, the characteristic grass.	Widespread.	pijang'-holo	—	—	—	—	—
185	*Microglossa densiflora* Hook. f.	Compositae.	Shrub.	Riverine.	Widespread.	—	—	—	—	—	—
186	*Mimusops densiflora* Engl.	Sapotaceae.	Tree.	Hard-pan and riverine in 9 and 7.	Widespread.	konze	mkonze	—	—	manha	—
187	*Mucuna* spp.	Papilionaceae.	Vigorous climbing herb.	Upland eluvial, in grass-jungle, and long-grassed *Combretum*.	Widespread.	—	—	upupa	—	—	Buffalo bean, velvet stinging bean.
188	*Ormocarpum trichocarpum* Harms.	„	Shrub.	Hard-pan, 9, 7.	Western, Lake and Central Provs.	lulamburi	—	—	—	kilumbu-lubu	—
189	*Ostryoderris Stuhlmannii* Dunn.	„	Medium-sized tree.	Eluvial, with erect Combretums and, in 9, 7, *Commiphora Fischeri* (107 above); in 4, with the Combretums and *Ac. pallens* (15 above).	Widespread.	nene, jundu	mnyenye	—	mejiula	mninga	Ash-like ostryoderris.
190	*Panicum maximum* Jacq.	Gramineae.	Tallish grass.	Widely spread through tree-shrub communities.	Widespread.	—	—	—	—	—	—
191	*Parinarium curatellaefolium* Planch.	Rosaceae.	Tree, medium to large.	Eluvial, esp. in parts of 6 and in 5, where l.d. or co-d.	Widespread.	—	mwula	mbura	—	—	—
192	*Paullinia pinnata* L.	Sapindaceae.	Large woody climber.	Riverine.	Widespread.	—	—	mfulu nyengoro	—	—	—
193	*Pavetta* spp.	Rubiaceae.	Shrubs, usually, large and small.	Various communities.	Widespread.	—	—	—	—	—	—
194	*Pennisetum purpureum* Schm.	Gramineae.	Tall, cane-like grass.	Riverine.	Mostly western T.	—	—	—	—	—	Elephant grass.
195	*Phoenix reclinata* Jacq.	Palmae.	Thicket-forming palm, not tall.	Rain forest margins, riverine.	Widespread.	—	—	—	—	—	Wild date palm.
196	*Phyllanthus discoideus* Mull.	Euphorbiaceae.	Coppicing shrub.	1, miombo (*Brachystegia–Isoberlinia*).	Widespread.	—	usenga	—	—	—	—

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197	***Phyllanthus Engleri*** Pax.	Euphorbiaceae.	Small tree.	Eluvial soil, with erect Combretums.	Widespread.	ngongondi	mngongondi	—	—	—	—
198	***Piptadenia Buchanani*** Baker.	Mimosaceae.	Very large tree.	Rain forest.	Eastern areas, T.	—	—	—	—	—	Rain forest piptadenia.
199	***Piptadenia Hildebrandtii*** Vatke.	"	Large tree.	Riverine.	Central and W. areas, T.	nata	mliaka	—	—	—	River piptadenia.
200	***Popowia obovata*** Engl. & Diels.	Anonaceae.	Luxuriant trailing shrub.	Thickets, esp. in fair rainfall areas, as in miombo, 1.	Central and Western areas of T.	—	msalasi	—	—	—	—
201	***Protea abyssinica*** Willd.	Proteaceae.	Shrub, evergreen.	Eluvial, upland, with erect Combretums, *Sizygium owariense*, *Faurea*, *Parinarium* and *Terminalia torulosa*.	Widespread.	—	—	—	—	—	Hairy sugar-bush.
202	***Protea chionantha*** Engl. & Gilg.	"	Shrub, evergreen.	" "	Widespread.	—	—	—	—	—	Smooth-leafed sugar-bush.
203	***Pseudolachnostylis maprounifolia*** Pax.	Euphorbiaceae.	Tree, small to medium.	1, miombo (*Brachystegia–Isoberlinia*).	Widespread.	—	mtunguru	—	—	—	—
204	***Pseudoprosopis Fischeri*** Harms.	Mimosaceae.	Coppicing shrub.	12, Central group in map, Itigi thicket.	Central Prov.	—	—	—	—	—	—
205	***Psidium Guyava*** L.	Myrtaceae.	Large shrub or small tree, evergreen.	Cultivated and forming thickets in savanna as an escape.	—	—	—	mpera	—	—	Common guava.
206	***Pteleopsis myrtifolia*** (Laws) Engl. & Diels.	Combretaceae.	Tallish tree, slender.	1, miombo, l.d. in colluvial interzone with *Lonchocarpus* (175 above), and Combretum, between the miombo proper of the eluvial slopes and alluvial enclaves carrying *Ac. usambarensis*, etc. Sometimes (N. Tanga) l.d. over larger areas.	Eastern areas.	—	—	—	—	mgovu	—
207	***Pteridium aquilinum*** Kuhn.	Ficales.	Herb (bracken).	Chiefly 10, also 5, but occurring even in Zanzibar.	Widespread.	—	—	—	—	—	Common bracken.
208	***Pterocarpus Bussei*** Harms.	Papilionaceae.	Tallish tree, slender.	1, miombo (*Brachystegia–Isoberlinia*), sometimes itself l.d.	Widespread.	nninga	mwininga	—	mwuininga	muhagata	Bloodwood.
209	***Pygeum africanum*** Hook. f.	Rosaceae.	Very large tree, evergreen.	Rain forest and ravine forest.	Widespread.	—	—	—	—	—	Rosaceous redwood.
210	***Pyrenacantha malvifolia*** Engl.	Icacinaceae.	Succulent climber.	Hard-pan Masailand, 9.	N. and E. Provs.	—	—	—	—	—	Rhino root.
211	***Raphia pedunculata*** Beauv. Madagascar.	Palmae.	Palm tree.	Riverine.	Lake and Eastern Provs.	—	—	mwale	—	—	Raffia palm.

212	***Randia Taylorii*** **sp. Moore.**	Rubiaceae.	Shrub to small tree.	Eluvial or colluvial, often with erect Combretums.	Widespread.	wocha-ngoko	mpongolo	—	mpegos	sewe	Taylor's Chevaux-de-frise.
213	***Rauwolfia inebrians*** **and** ***inequalis.***	Apocynaceae.	Large tree.	Riverine and ravine forest and rain forest outskirts and clearings.	Widespread.	—	—	—	—	—	—
214	***Rhamnus prinoides*** L'Herit.	Rhamnaceae.	Shrub, evergreen.	Subtropical rain forest, outskirts.	Widespread.	—	—	—	—	—	—
215	***Rhoicissus*** spp.	Ampelidaceae.	Climbing plants.	Various, from rain forest (*R. capensis*) to grass-land.	Widespread.	—	—	—	—	—	Grape-vine lianas.
216	***Rhus glaucescens*** A. Rich.	Anacardiaceae.	Large coppicing shrub, evergreen.	*R. cuneifolia* d. in thickets, often with *Carissa edulis*, under fair rainfall or in mist-belts; with *Brachystegia microphylla* on scarps, l. in 6 and 1, esp. in 11 and (in N.W.) 3.	Widespread.	—	—	mbungala	—	—	Glaucous rhus.
217	***Ricinus communis*** L. Tropics generally.	Euphorbiaceae.	Straight, soft-stemmed shrub.	Cultivated and escape round old cultivation.	Widespread.	mnare	—	mbarika	—	—	Castor-oil plant.
218	***Sanseviera*** spp.	Liliaceae.	Succulent.	Thickets generally in 7, 9, 8.	Widespread.	ng'honge	—	mkongo	i(ch)onge	ukongi	"Wild Sisal."
219	***Sesbania Sesban*** (L.) Merv.	Papilionaceae.	Small tree.	Chiefly lacustrine.	Widespread.	—	—	—	—	—	—
220	***Swartzia madagascariensis*** Desv.	Caesalpiniaceae.	Tree.	1 miombo (*Brachystegia–Isoberlinia*).	Central and W. areas, T.	—	kasanda	—	—	—	—
221	***Sclerocarya birrea*** Hochst.	Anacardiaceae.	Large tree.	7 and 8 in particular.	Widespread.	ngongo	mngonho	—	mhui	mgongo	—
222	***Syzygium owariensis*** Benth.	Myrtaceae.	Small to medium tree.	Upland eluvial savannas, as 5, with *Protea*, *Faurea*, *Parinarium*; and (l.) in 6.	Widespread.	—	—	—	—	—	Savanna eugenia.
223	***Syzygium guineense*** (Willd.) D.C.	"	Very large tree, evergreen.	Rain forest, temperate rain forest, remnant thickets of latter (as in Bereku, Kondoa) and evergreen riverine.	Widespread.	—	kizambarai	—	—	—	Rain-forest eugenia.
224	***Smilax Kraussiana*** Meissn.	Liliaceae.	Climbing thorny plant.	L. in 5 and elsewhere. Often with bracken.	Widespread.	—	—	—	—	—	—
225	***Spathodea nilotica*** Seem.	Bignoniaceae.	Largish tree, evergreen.	Rain forest (outskirts and secondary), ravines and tall grass-jungle.	Uganda and W. Kenya.	—	—	—	—	—	Nandi flame.
226	***Sporobolus*** spp.	Gramineae.	A small grass.	Hard-pan.	Widespread.	—	—	—	—	—	Drop-seed grass.
227	***Sterculia appendiculata*** K. Schm.	Sterculiaceae.	Very large tree.	Riverine and rain forest, thicket under fair rainfall and in cultivated areas.	Eastern areas, T., back to Kilosa.	—	—	—	mfuno	mglude	Giant yellow-bark sterculia.

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228	*Strychnos heterodoxa* Gilg.	Loganiaceae.	Largish tree.	Eluvial soil in 7, 9 with erect Combretums, *Commiphora Fischeri*, etc.	Widespread.	mpande-pande	mgwegwe	—	mpande	—	Black-berried strychnos.
229	*Strychnos pungens* Sol.	"	Large shrub.	Eluvial or colluvial with Combretums in 1, miombo.	Central and W. areas, T.	mkogo	—	—	—	—	Spike-leafed strychnos.
230	*Stereospermum Kunthianum* Chan.	Bignoniaceae.	Small tree, handsome, mauve bell flowers.	1, miombo, often as described for 229; or on alluvium.	Widespread.	—	—	—	—	—	—
231	*Synadenium Grantii* Hook. f.	Euphorbiaceae.	Small tree, succulent.	Hard-pan, Masailand.	Widespread.	—	—	—	—	mlua	Blinding milk-wort.
232	*Tamarindus indica* L.	Caesalpiniaceae.	Medium tree.	Thickets riverine and other, in savanna and cultivation steppe (because unfelled), scattered generally in 7 and 9, as interzone tree in 1. Often under a baobab (Zambezi valley).	Widespread.	shishi	mshishi	mkwaju	mkwaju	mwazu	Tamarind.
233	*Teclea nobilis* Del.	Rutaceae.	Tall shrub, evergreen.	Thickets on hills, in 7 and 9, in lacustrine forest Uganda, in Rutaceous high thicket, Moshi.	—	—	—	—	—	—	—
234	*Teclea swynnertonii* Baker fil.	"	Large tree.	Trop. rain forest.	S. Rhodesia.	—	—	—	—	—	—
235	*Teclea glomerata* Verdoorn.	"	Small tree.	Hard-pan, thickets.	Central and W. areas, T.	nlungusi-giti	mlungu-lungu	—	—	—	—
236	*Tecoma stans* Juss. N. and S. America.	Bignoniaceae.	Large shrub or small tree.	Cultivated for ornament.	Over wide range, from 6 to 9. [N. and S. America.]	—	—	—	—	—	Erect ornamental tecoma.
237	*Tectona grandis* L. East India, Burma.	Verbenaceae.	Large tree.	Cultivated.	Tanga Prov. esp.	—	—	msaji	—	—	Teak.
238	*Terminalia sericea* Burch.	Combretaceae.	Medium tree.	Mainly 1, miombo areas, on eluvial and colluvial with erect Combretums, sometimes in 7; survives exterminated miombo and is often d. in abandoned native cultivation.	Widespread.	nzima	mzima	—	mpuru	mvumba	Common terminalia.
239	*Terminalia Stuhlmannii* Engl.	"	Smallish tree.	Hard-pan, in thickets and otherwise in 7, 9.	Central and W. areas.	ngiri	—	—	mkiampa	—	Hard-pan terminalia.

240	*Terminalia torulosa* F. Hoffm.	Combretaceae.	Medium tree.	Eluvial uplands often d. or co-d. with erect Combretums, *Protea*, *Faurea*, *Sizygium*, *Parinarium*.	Widespread.	—	mkelenge	—	—	—	Broad-leafed terminalia.
241	*Thunbergia alata* Boj.	Acanthaceae.	Climbing herb.	Rain forest margin.	Widespread.	—	—	—	—	—	Black-eyed Susan.
242	*Trema guineensis* Fic.	Ulmaceae.	Medium tree.	Rain forest outskirts and openings, secondary rain forest.	Widespread.	—	—	—	—	—	—
243	*Uapaca guineensis* Muell. Arg.	Euphorbiaceae.	Tree, evergreen.	—	—	—	—	—	—	—	—
244	*Uapaca Kirkiana* Muell. Arg.	"	Small to medium tree, evergreen, large leathery leaves.	1, miombo, forming pure groves on eluvial, sometimes of many square miles. Elsewhere (5) small groves or scattered in the miombo bush or (S.E. 1) as rings round small mbugas.	Just back of Dar-es-Salaam, in E. areas scarce, in W. much commoner, becoming abundant in South and one of the dominant forms in Nyasaland and Rhodesias.	—	—	—	—	—	—
245	*Uapaca nitida* Muell. Arg.	"	Small to medium tree, evergreen, small leaves.	Much as above, and with it, but nowhere forming such great groves.	As above in Tanganyika, except more frequent in E., as in foothills N.E. of Kilosa.	—	—	—	—	—	—
246	*Uapaca sansibarica* Pax.	"	Small to medium tree, evergreen.	Similar conditions and often with *Kirkiana*, but less abundant. Sometimes (P.E.A.) forming dense groves on colluvial and hill-bases round mbugas.	Western 1, chiefly.	—	—	—	—	—	—
247	*Usnea* sp., "Old Man's Beard."	—	Dependent lichen, epiphyte.	Rain forest, esp. temperate; on *Brachystegia microphylla* on upland, and *Acacia hebecladoides* in Ankole.	Widespread.	—	—	—	—	—	Old man's beard.
248	*Vernonia podocoma* Sch. Bip.	Compositae.	Large shrub.	Rain forest margin and in tall herbage in potential rain forest areas.	Widespread.	—	—	—	—	—	Cherry-pie Vernonia.
249	*Vernonia senegalensis* Less.	"	Small tree or large shrub.	Riverside land, more or less alluvial.	Widespread.	—	—	—	—	—	Bitters tree.

No.	Species	Family or Sub-family	Form	Community or habitat	Distribution in Tanganyika as known [or exotics, origin]	Kisukuma (Lake Province)	Kinyamwezi (Western Province)	Kiswahili (Coastal)	Kinyaturu (Singida)	Kiluguru (Morogoro)	English Equivalent, actual or suggested
250	***Vitex Cienkowskii*** **Kotch & Peyr.**	Verbenaceae.	Tree, medium.	Margins of some alluvial flats, colluvium under scarps (Nguru), grass-jungle on rich doleritic soil (P.E.A.), etc.	Widespread.	mpulu	mfulu	—	—	mgobe	—
251	***Vitex Hildebrandtii*** **Vatke.**	"	Small tree.	Eluvial or colluvial, with erect Combretum.	Widespread.	nsungwi	—	—	—	—	—
252	***Zizyphus mucronata*** **Willd.**	Rhamnaceae.	Tree, medium to small.	Riverine (7, 9) or in thickets—or on ant-heaps under fair rainfall elsewhere (*e.g.* 1).	Widespread.	ngugunu	kagoele	—	mungugunu	muhingi	Buffalo-horn.

APPENDIX 8.

SOME DETAILS OF THE EXPERIMENTS IN POISONING SAVANNA AND RAIN-FOREST TREES AND THICKET.

By S. Napier-Bax, Senior Field Officer, Tsetse Research Department, Tanganyika Territory.

1. Introducing the poison.

Syringes of various types, veterinary (metal and glass), Maw's pattern (glass and vulcanite) and, later, enamel coffee-pots were tried out and discarded. Engineers' oilcans were fairly successful, but finally a suggestion by G. T. Wheeler, a beer-bottle fitted with a cork through which a glass tube (drawn to a fine aperture at each end) passed, was adopted and found very satisfactory.

2. Poisons.

(a) *Arsenic pentoxide.*

Arsenic pentoxide has been found to be the most effective. Successful results have been obtained by the frill method on the following trees : *Commiphora Schimperi*, *C. ugogensis*, *Lannea humilis*, *Acacia Senegal*, *A. spirocarpa*, *A. Kirkii*, *A. formicarum*, *A. Seyal*, *Isoberlinia globiflora* and *Brachystegia* spp. A concentration as high as 10 lb. to the gallon of water is necessary in the case of *C. Schimperi* for fairly quick results and in the case of *Lannea humilis* too, but even this concentration affects the roots and stem of *Isoberlinia globiflora* and *Brachystegia* spp. but slowly. *A. spirocarpa* has been dealt with successfully with as low a strength as 3 lb. to the gallon, and it is possible that the other acacias would respond to a similar strength, although experiments have only been carried out with the 10 lb. strength.

Other savanna trees on which this poison has been tried are the three Combretums, *C. apiculatum*, *C. splendens*, and *C. Zeyheri*. Even concentrations higher than 10 lb. failed to kill these, although the poisoning was responsible for a certain suppression of regeneration—coppicing.

A concentration of 4 lb. to the gallon was tried on a number of rain-forest genera. The sugar method was employed, as Dr. Phillips had found this quite successful in South Africa under similar conditions. The trees poisoned included :—*Ekebergia* sp., *Apodytes dimidiata*, *Albizzia gummifera*, *Eleodendron* sp., *Calodendron capense*, *Nuxia* sp., *Syzygium guineense*, *Podocarpus milanjiana*, and *Podocarpus gracilior*. Results were most disappointing, a greater or less barber-pole effect being produced in stem and roots, but no tree being killed or really seriously damaged.

Arsenic pentoxide inserted into frills and auger-holes in the solid state was not found to be so successful as when in solution in water.

Colloidal suspensoids of this poison have been made with paraffin-soap, glue, gum arabic and native sugar to increase the "spread," vaseline has been used for aiding the penetration and sodium silicofluoride was tried with the object of increasing the availability of the arsenic. But none of the foregoing were markedly superior to arsenic pentoxide in water.

(b) *Sodium arsenite.*

The commercial form of this poison was tried on *Commiphora Schimperi*, but was not so successful as arsenic pentoxide. Samples made from two different recipes also failed to equal the results with arsenic pentoxide.

The effect with the commercial form used "solid" (unmixed with water) in the "frills" was poor.

(c) *Calcium arsenite.*

At a strength of 4 lb. to the gallon of water and used in both frilled and augered *Commiphora Schimperi*, the effect was negligible in the former case and in the latter indiscernible.

(d) *Arsenic trichloride.*

This was used at the rate of 15 cub. cms. to the auger-hole on *C. Schimperi* and in a further experiment was mixed with an equal volume of paraffin and a similar amount introduced into the auger-hole. In both cases the results were disappointing.

(e) *Arsenious oxide.*

This poison was tried in the solid form, an experiment being made on frilled *C. Schimperi*. The effect was slight. In another experiment a colloidal suspension (4 lb. = 1 gal.), was made with the aid of gum arabic and was tried on trees of the same species. The effect was again but slight.

(f) *Arsenic trisulphide.*

On frilled *Isoberlinia* spp. no effect at all was seen; on *C. Schimperi* there was a slight effect.

(g) *Lead arsenate.*

2½ lb. to 1 gallon of water had no effect at all on *C. Schimperi* when introduced into auger-holes. On frilled *C. Schimperi* the effect was slight.

(h) *Potassium dichromate.*

A solution of this, 1 lb. to the gallon of water, was quite unsuccessful on both frilled *Isoberlinia* spp. and *C. Schimperi*. Used at the same strength but with one-hundredth of its volume of strong commercial sulphuric acid added the effect on both trees was very slight. Used in the solid form on frilled *C. Schimperi* it was unsuccessful.

(i) *Sodium chlorate.*

When this poison was used at the strength of ½ lb. to one gallon of water there was but little effect on frilled *C. Schimperi* and none at all on *Isoberlinia* spp. In the solid form once again there was little effect on *C. Schimperi* and none on *Isoberlinia* spp.

(k) *Copper-aceto-meta-arsenite.*

On frilled *C. Schimperi* at the rate of 4½ lb. to the gallon of water there was little effect.

(l) *Copper sulphate.*

Employed on frilled *C. Schimperi* this salt, at 4½ lb. to the gallon of water, gave irregular but often effective results. A lower concentration gave poorer results as did a stronger one of 9 lb., which of course was no longer a solution

but a paste. The $4\frac{1}{2}$ lb. solution swabbed on to the stumps of felled *C. Schimperi* was not very effective.

Tried on frilled *Combretum apiculatum* and *Isoberlinia* spp. there were no results but the $4\frac{1}{2}$ lb. solution once more gave irregular but often effective results on *Acacia Senegal.*

(m) *Commercial sulphuric acid.*

This tried on frilled *C. Schimperi* was often effective in killing it, but on *Combretum apiculatum* the effect was slight. Diluted to a strength of 15% it was still fairly effective on *C. Schimperi.*

(n) *Potassium nitrate.*

Inserted "solid" in the frills and auger-holes of standing *C. Schimperi* there was but a very slight effect, on *Isoberlinia* spp. no effect was discernible.

When *C. Schimperi* were felled and the stumps augered and the poison inserted the effect was increased.

3. Thicket growth.

Spraying and swabbing experiments with arsenic pentoxide have been carried out but the method has been found very expensive and generally unsuccessful.

APPENDIX 9.

NOTE ON THE GAME SANCTUARIES SHOWN ON MAP 7.

BY C. F. M. Swynnerton.

It is important to preserve for study and posterity the natural animal communities each in its natural vegetational setting. The preservation of the general vegetation communities, which is part of the plan, is a matter of great interest in itself and requires far more "management." I recommended the first Reserves, selecting them from those created under the German régime each with a special object, while stating that a thorough vegetational and faunal survey would be necessary as the basis for a final choice. The object is in some cases stated on the map. The first two to be mentioned below are more recent creations.

(a) *The Plains and nyika communities.*

The Serengeti complete reserve and the Ngorongoro Crater Reserve—I prefer the word sanctuary—serve mainly the plains game, though the Serengeti serves also to some extent the game of the western (less extreme) dry thorn-bush—NY^2, with roan and topi.

The Natron and Northern Railway sanctuaries serve the drier, semi-desert nyika without roan or topi, but with oryx, gerenuk, vulturine guinea-fowl and their associates.

To the Serengeti "closed reserve" (pl. 2) I have in the map given the more accurate title of "Preserve"—for much shooting is allowed to take place in it on the part of approved licensees. The perpetuation of this area, with more limited shooting and an ample enlargement of the sanctuaries attached to it, is a step that will adequately preserve for posterity the spectacle of the plains game of Africa, as it was before the advent of man. Some mining is penetrating the preserve to-day, but with cattle meat used for the mining natives instead of game meat—and the cattle should obviously be used—it would seem likely that the wild animals, and this great National Park of the future, will outlast the high price of gold and with it most of the mining.

(b) *The miombo community.*

The miombo community is provided for principally by the Saba Reserve, which is valuable. Useful variations of the type are to be found in the north of the Selous Reserve and in the Katavi Reserve, were this last extended. At the present it is a huge mbuga, very attractive to the game at the period of the young shooting grass and attractive to zebra and topi at all times except when swampy. In order to provide its animals with all their requirements and to prevent them from living outside it for most of the year, it needs a block of the uninhabited miombo country alongside.

(c) *The rain-forest community.*

The rain-forest community is protected by the Kilimanjaro and Meru Reserves, but it is unfortunate that the tree-hyrax has been excepted from this

protection on Kilimanjaro, and is hunted intensively for its skin, while the hunters disturb and probably destroy other animals also. Blue duiker has probably nowhere sanctuary protection in Tanganyika.

(d) *The dry thicket communities.*

There is little special sanctuary for these.

To some extent the thicket communities, and especially their "heavy" species, elephants more particularly, are provided for in the very valuable Selous sanctuary. I formed this by joining the old German Mahenge and Mohoro Reserves in order to include in it Selous' grave at Behobeho between them. Riverine species are protected also in the fine rivers which bound this sanctuary.

(e) *The swamp communities.*

These are incompletely provided for. Part of the small Lake Rukwa reserve, not shown in the map, is of use. Some swamp—and some puku—exist in the Selous Reserve, but one of the great swamp-plains of Mahenge, with puku in herds of hundreds, is needed if it can be spared from future rice-growers. The Kagera and Melagarori swamps offer possibilities.

(f) *The preservation of animals at the extremes of their ranges.*

This is a matter of considerable scientific interest and has been insufficiently borne in mind. Sable antelopes find their northernmost point, it is believed, in Uzinza, in Mwanza District. Yet they have here, with greater kudu and the other game locally present, been subjected to intense persecution by organised native hunting. Much-needed convictions were obtained here lately by the Game Department.

The Logi Reserve, now abolished, was of interest in a similar connection. Owing to native activities this outpost is now unlikely to survive, and the southernmost point of Grant and Oryx will have been pushed fully eighty miles north, to the Mlali plains near Mpapwa.

APPENDIX 10.

A NOTE ON THE DISTINCTIVE CHARACTERS OF THE EAST AFRICAN SPECIES OF THE GENUS *GLOSSINA* WIEDERMANN, 1830, AND OF THEIR PUPAE, SPECIALLY PREPARED FOR USE BY WORKERS IN THE FIELD.

By C. F. M. Swynnerton.

1. The difference between tsetse flies and other flies.

In the resting position the wings of a tsetse fly overlap each other like the blades of a closed pair of scissors, but they coincide completely, and lie flat. They show no separate points. The wings are long and project well beyond the abdomen, which they hide. They therefore give the fly a very elongated appearance.

The wings of species of spotted " cleg " belonging to the genus *Haematopota*, Meigen, 1803, meet above the middle line of the abdomen, and slope off to each side like a roof. They are usually closely mottled with black or grey. In the smaller, clear-winged species of " horse " or " hippopotamus " fly belonging to the genus *Tabanus* Linn., 1758, which are frequently mistaken for tsetse flies, the points of the wings, which lie flat like those of tsetse flies, are well separated.

A striking peculiarity in the wing of tsetse flies, in which they differ from all other flies, is the hatchet-like form of the cell or space in the middle of the wing, which results from the course of the zigzag fourth longitudinal vein.

2. The external difference between the sexes of tsetse flies.

The male has a convex knob (the hypopygium), shown in pl. 21, on the under surface of the apex of the abdomen. This knob can be turned back to reveal the claspers and other parts the form of which affords useful aid in the classification of the species.

In the female the under surface of the apex of the abdomen is, to the naked eye, plain and smooth.

3. The three groups of tsetse flies (Newstead's classification).

(*Note.*—The superior claspers pressed down after the hypopygium of the male has been turned back, show as two points or claws, especially strongly in the *fusca* and *palpalis* groups.)

(a) *The* fusca *group.*

1. Size: Large, wing length 11 to 13·5 mm.
2. Colour: Brown or pale brown. Hind tarsi not entirely dark brown or black above; upper surface of abdomen not contrastedly banded.
3. Claspers: No connecting membrane between the claspers, which stand out long, narrow, pointed and free.

East African species: *G. brevipalpis*, *G. fusca*, *G. fuscipleuris*, and *G. longipennis*.

(b) *The* palpalis *group.*

1. Size: Small, wing length given below.
2. Colour: General colour very dark in *G. palpalis*, hind tarsi entirely dark brown or black above; upper surface of abdomen contrastedly banded in *G. tachinoides* (W. Africa and Arabia) only.
3. Claspers. Not unlike those of the *fusca* group, but, except for their points, connected by a membrane which is deeply divided in the middle.

East African species: *G. palpalis* in its forms *G. p. fuscipes* (of Lake Victoria and the Nile system) and *G. p. martinii* (of Lake Tanganyika).

(c) *The* morsitans *group.*

1. Size: Medium (*G. pallidipes*), to small (*G. morsitans*, *G. swynnertoni* and especially *G. austeni*), wing lengths given below.
2. Colour: Except in *G. austeni* hind tarsi not entirely dark brown or black above; upper surface of abdomen contrastedly banded except in *G. austeni* (see below).
3. Claspers: Completely united by a membrane, narrow at their bases and greatly broadened at their extremities where their inner angles nearly meet. Claw, practically absent or reduced to a "marginal tubercle," more prominent in *G. pallidipes*, on the edge of the broadened end.

4. Keys to the east African species of the genus *Glossina* Wiedermann.

(a) *The east African species of the* fusca *group* (*after Austen and Newstead combined*).

Palpi (enclosing proboscis) relatively short, length not exceeding transverse diameter of head by more than one-ninth of their length, general appearance light or medium brown, wings lightly tinged brown, anterior transverse vein darkened or not. Thorax with or without distinct dark spots . . 1.

Palpi relatively long, exceeding diameter of head by one-third to one-sixth of their length, general appearance of the fly dark brown, wings strongly tinged dusky, anterior transverse vein not darkened (*i.e.* no dark brown spot on wing), thorax without distinct dark spots . . . . 2.

1. a. *Thorax with four distinct dark spots, occasionally more.*
General colour light, pinkish grey-brown (isabelline); abdomen (unbanded) often nearly orange in colour . . . . (i) *G. longipennis.*
b. *Thorax without distinct dark spots.*
General colour medium brown, wings of both sexes with the thickened part of the *anterior transverse vein darker than the others*, providing the impression of a dark brown spot on the wing (ii) *G. brevipalpis.*
2. a. Sides of thorax (pleurae) dark grey, hind coxae (short leg-joint next body) mouse-grey . . . . (iii) *G. fuscipleuris.*
b. Sides of thorax light pinkish-grey (isabelline), hind coxae buff (iv) *G. fusca.*

(b) *The east African species of the* palpalis *group.*

One species only, *G. palpalis* (species (v)), small (wing length 6·5 mm. in a small male to 8 mm. in the female), *very black* in general colour. Upper surface of thorax very dark iron-grey with the longitudinal brown markings common to most species of tsetse fly. No contrasted banding on abdomen: upper surface of abdomen black-banded on a deep iron-grey ground, the black banding monopolising nearly all the space. The hind edges of the segments often narrowly paler. Wings dusky.

The species occurs in two main forms which are definitely distinguishable

by their genitalia only—*G. p. palpalis* of west Africa and *G. p. fuscipes* of Lake Victoria and the Nile region. The form inhabiting the shores of Lake Tanganyika has lately been described by Zumpt as *G. martinii*. It is very slightly different from the two main forms and in its differences it is intermediate between them. The inferior claspers of typical *G. p. palpalis* and the form *martinii* possess a " heel " at their bend which *G. p. fuscipes* lacks. On the other hand the bay in the inner margin of the inferior clasper both of *martinii* and *fuscipes* is deeper and narrower than in that of *G. p. palpalis*.

(c) *The east African species of the* morsitans *group.*

1. *All segments of hind tarsi dark brown.*
   Upper surface of abdomen bright ochreous-tawny with traces of dark transverse bands, usually widely interrupted and not sharply defined. The ochreous-tawny tinge extends often to the lighter portions of the thorax.
   Size small, wing (long for bulk of body) from 7 to 8 mm. . (vi) *G. austeni*.
2. *Hind tarsi not entirely dark brown or black above; last two joints of front and middle tarsi without contrasted clove-brown or black tips, the latter light brown or pale.*
   Dark bands on ochreous-tawny upper surface of abdomen varying from black to brown, and appearing commonly as though showing through amber or varnish; occasionally much reduced. Underside and sides of body, and legs, generally pale in appearance.
   Size medium, wing length 8·7 to 10 mm. Male hypopygium small (vii) *G. pallidipes*.
3. *Hind tarsi not entirely dark brown or black above but last two joints of front and middle tarsi with sharply contrasted clove-brown or black tips.*
   The black banding on the pale ground of the upper surface of the abdomen appearing as though on the surface, not, as usually in *pallidipes*, showing " through."
   Size between species (vi) (*G. austeni*) and species (vii) (*G. pallidipes*), wing length 7 to 9·1 mm. Male hypopygium large—*see* pl. 21.
   (*a*) Dark bands on upper surface of abdomen, shallower, usually, well separated and with their ends always tapered off, strongly, or less strongly, from below, so that they form quasi-crescents. Ground-colour, usually ochreous-fawn, often bright, sometimes greyer. Second (the largest) abdominal segment, as a rule longer, measured from front to back, in relation to its width from side to side . . . . (viii) *G. morsitans*.
   (*b*) Dark bands on upper surface of abdomen deeper and having their inner ends, next to the pale median line, close together, *sharply defined and square*. Ground-colour mostly dull grey with the median line (rarely the rest) tinged with fawn. Second abdominal segment as a rule shorter, measured from front to back, in relation to its width from side to side . . . (ix) *G. swynnertoni*.

See pl. 21, in which, however, the contrast in the amount of black, and in the depth of the second segment, is somewhat extreme.

For fuller keys and descriptions, comprising all species of *Glossina*, the following works should be consulted: Austen (1922), Newstead (1934), Austen and Hegh (1922), and Hegh (1929).

5. Key to the pupae of the east African species of the genus *Glossina* Wiedermann.

The identification of the pupae of the different species of *Glossina* is assisted by the differing shape of the two conspicuous lobes at the posterior end and of

the space between them. Material regarding the pupae of *G. fuscipleuris* and *G. longipennis* is unfortunately not available. The following key deals, therefore, with seven only out of the nine east African species. Of some of the others the material available at writing is scanty, so that the measurements given may not include the extremes.

1. Large, 7 to 8 mm. long . . . . The *fusca* group.
   (*a*) Lobes hemispherical, widely divergent, with a very open V-shaped space between . . . . (i) *G. brevipalpis.*
   (*b*) Lobes almost parallel with the axis of the body, space between them a shallow horseshoe . . . . (ii) *G. fusca.*
2. Small, 5–7 mm. . . . . The *palpalis* and *morsitans* groups.
   (*a*) Space between lobes a broad horseshoe.
      a′. Lobes large. Outside measurement across them up to 1·75 mm.
         a″. Puparium larger, broader, length 6–7, width 3·6–4 mm. (iii) *G. pallidipes.*
         b″. Puparium small, narrow, length 5–5·5, breadth 2·25–2·5 mm., the lobes looking particularly large on so narrow a body . . . . (iv) *G. austeni.*
      b′. Lobes smaller. Outside measurement across them less, up to 1·5 mm.
         c″. Puparium small, but wider than in (iv), length 5–6 mm., breadth 3·4–3·5 mm. Posterior end of puparium, next the lobes often less rounded, tending to slope away (v) *G. swynnertoni.*
   (*b*) Space between lobes narrow.
         d″. Puparium shaped as in species (v) (*G. swynnertoni*), but posterior end of puparium, next the lobes, full and rounded, length 5–6 mm., usually in *G. morsitans*, 5·5–6·1 in *G. palpalis*, by 3·2–3·8 in either in width.
            a‴. Lobes full and rounded, usually slightly convergent, the opening between them well rounded (vi) *G. palpalis.*
            b‴. Lobes small to very small, slightly divergent or, at most, vertical, the space between them a narrow U or a V with a slightly rounded apex (vii) *G. morsitans.*

Note on G. morsitans *and* G. swynnertoni.

It should be noted that *G. morsitans* and *G. swynnertoni* differ not only in coloration and in length of the second segment in the imago and in the shape of the pupa, all as described above, but also in habitat and habits, as is shown on pp. 58–60 and 85–89 respectively.

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PLATE 1.

The dry thorn-bush, savanna wooding of *Acacia–Commiphora*–other-genera, infested with *G. swynnertoni*.

Photograph on the Serenera stream, Serengeti plains, by Mrs. M. S. Moore. For the other major savanna–woodland formation, the miombo, *see* fig. 8.

The dry thorn-bush, savanna wooding of *Acacia–Commiphora*–other-genera; map 1 and pp. 85–89.

PLATE 2.

Open grass savanna.

Serengeti plains, uninhabitable by tsetse flies but peopled with vast numbers of game animals and (Serengeti), a potential site for the finest of all National Parks. Wildebeests in the foreground, dry thorn-bush in the distance. Photograph by Mrs. M. S. Moore.

Open grass savanna. The Serengeti plains and their game.

Plate 3.

Concurrence of requirements of the tsetse fly.

Fig. 1. The anatomy of a *G. morsitans* fly belt.

Miombo wooding from the air, showing concurrence of its vegetational requirements as a need of the tsetse fly and the anatomy of a *G. morsitans* fly belt.

Vertical photograph in the small "Racquet" fly belt, near Kazikazi, at the leafless season (for map, *see* pl. 20, fig. 2). **A** is the miombo wooding (*Isoberlinia–Brachystegia*), which is the "home" of the flies, in which they rest and breed; **B**, ground showing grey, is a narrow short-grassed, open, "hard-pan" drainage line dotted with small trees of *Lannea humilis* (mtinji) and *Commiphora subsessilifolia*, which the flies resort to when hungry, as a feeding-ground. **C**, with bare soil shining white, is the interzone on colluvial soil of (in this case) *Combretum Zeyheri*, *Terminalia sericea*, *Albizzia Harveyi*, and *Cassia abbreviata* with some *Commiphora ugogensis*, which, from recent observations, seems likely to be essential to the existence of permanent fly-concentrations. At the junction of the interzones and hard-pan are to be seen typical small hard-pan thickets of *Combretum parvifolium*. On the top margin, near the right-hand corner, is a piece of old cultivation reverting to bush.

This photograph and the next also illustrate the high recognisability of vegetation types from the air and the very great value to tsetse work of aerial reconnaissance.

Fig. 2. The anatomy of a *G. swynnertoni–G. pallidipes* fly belt.

Dry thorn-bush or nyika from the air, showing again "concurrence of requirements" and the anatomy of a piece of *swynnertoni–pallidipes* country at the south-east corner of the Huruhuru Plains, Shinyanga (map 2).

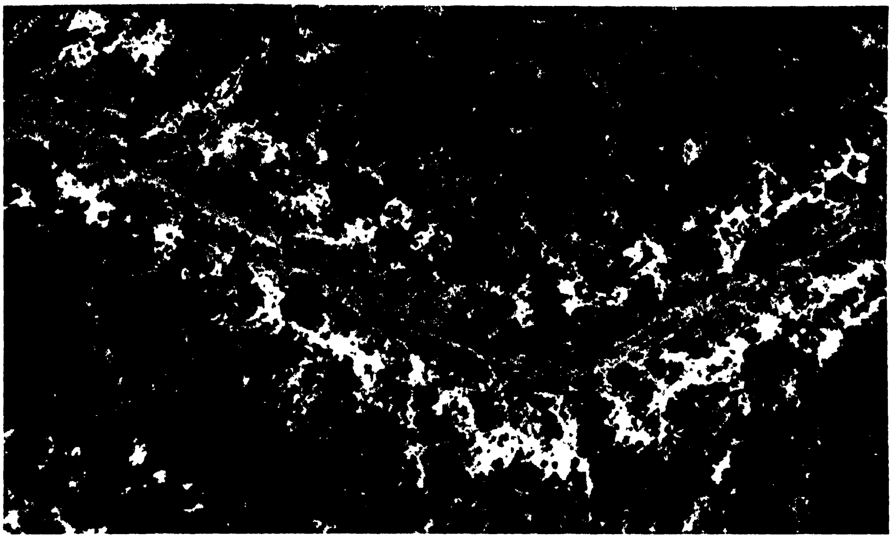
A is the general eluvial-soil wooding of the "thorn-bush" described in the text and is the "home" of *G. swynnertoni*, in which it rests and breeds during a part of the year in particular.

B, south-east corner of the great plains, is an open "mbuga" or "vlei" (grassland wet in the rains), with wooding of small gall-acacias (*A. drepanolobium*—"ilula") showing clearly: this is a definite "feeding-ground" of the hungry flies, which frequent or range its margin and fly to food animals in it. They infest the gall-acacias where these are within range of the normal home, but not otherwise.

C represents hard-pan patches and strips in which the flies both live and feed—very open (therefore serving as feeding-ground) but carrying small thickets and scattered trees of *Commiphora Schimperi*, *Lannea humilis*, and *Acacia drepanolobium*, which qualify them to be a "home" also. During part of the year they carry most of the fly population.

D is an extensive hard-pan area with some eluvial elements dotted through it on ant-heaps and other slightly raised patches. Much of Block 9 (the chief game experiment block) is like this and it represents what is sometimes called a "spread centre," difficult to deal with.

E is riverine thicket, the rest-haunt and breeding-place of *G. pallidipes*, which, however, searches for its food in all the other types shown, particularly in the feeding-grounds of the other flies.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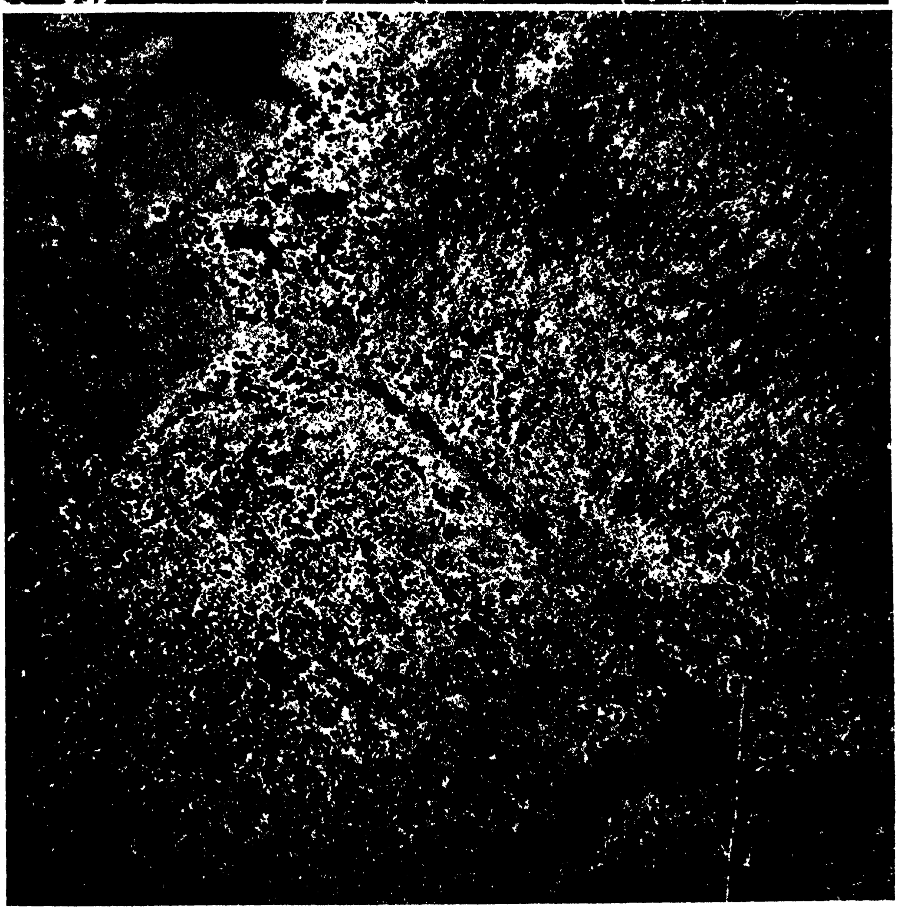
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Concurrence of requirements of the tsetse fly. Fig. 1, anatomy of a *G. morsitans* fly belt; fig. 2, anatomy of a *G. swynnertoni*-*G. pallidipes* fly belt.

PLATE 4.

Concurrence of requirements of two species of tsetse fly.

Riverine or "galling" thicket in the background, such as *G. pallidipes* needs for its rest-haunt and breeding-ground. Open alluvial mbuga in front, searched marginally for food. On the right, dry thorn-bush savanna of *Acacia spirocarpa*, etc., such as is used by *G. swynnertoni* and, if a good thicket base is available, by *G. pallidipes* also. On the Serengeti plains, photograph by Mrs. M. S. Moore.

Concurrence of requirements for two species of tsetse fly.

PLATE 5.

Habitats of *G. swynnertoni* and *G. pallidipes*.

FIG. 1. On the eluvial soil of the thorn-bush in Block 4B in Shinyanga (map 2), normally burned every year. *Commiphora Fischeri* predominating (left and background); *Acacias* and thickets present. A " home " of *G. swynnertoni*.

FIG. 2. Typical *Acacia* wooding on limonite or hard-pan. With thicket, the hard-pan type is used by *G. swynnertoni* both as a home and as a feeding-ground, without it as feeding-ground only. Experiments in clearing the hard-pan strips only were successful in expelling the flies from the piece of country at large.

FIG. 3. In Nindo, Block 13, Shinyanga, in 1923, map 2; wooding of *Strychnos heterodoxa*, *Ostryoderris Stuhlmannii* and *Combretum Zeyheri*, with thickets. " Home " of *G. pallidipes* and *G. swynnertoni*, both at that time abundant there. Game exceedingly scarce.

FIG. 4. Semi-desert *G. pallidipes* country, below Pare Mountains, much *Sanseviera*, fleshy *Crassulaceae*, *Adenium*, *Euphorbia*, and bare ground. Suited also to *G. longipennis*.

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Habitats of *G. swynnertoni* and *G. pallidipes.*

PLATE 6.

Concurrence of requirements for three species of tsetse fly produced by the activities of man.

The species here concerned are *G. pallidipes*, *G. brevipalpis*, and *G. austeni*. View from the East African Agricultural Research Station at Amani, to illustrate the effect of the free interspersal of vegetational types brought about by the invasion of rain forest by man. The rain forest here is everywhere broken up by cultivation and fallow and the types—savanna wooding (*e.g.* half left), open grass and regenerating rain forest—which follow abandoned cultivation. Unbroken dense rain forest is hardly penetrated even by such tsetses as *G. austeni* and *G. brevipalpis*; but the marginal contacts created in the area shown, are, so far as search has gone, infested practically throughout. Photograph by A. A. le G. Worsley.

Concurrence of requirements for three species of tsetse fly produced by the activities of man.

PLATE 7.

Screens and traps for the capture of tsetse flies.

FIG. 1. Our hand-catching screens of 1922–23, used with bird-lime or carried. These screens (like bait-cattle) are very attractive to the female flies which come little to man, and the small boys who carry them catch the flies off them.

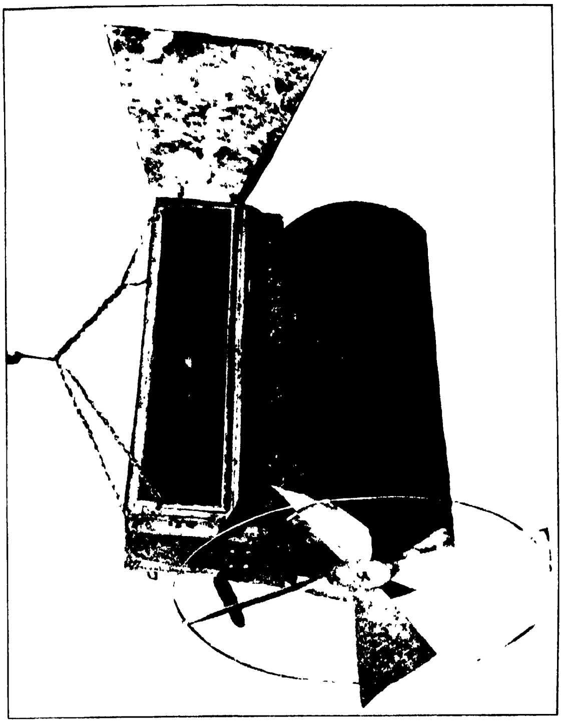
FIG. 2. A Harris Trap and Jackson's "JV" Trap in feeding-ground 2 of *G. pallidipes* in Block 9, Shinyanga.

The Harris Trap is a dark chamber which the flies **enter** from below, through an opening that runs the length of the "belly" of the "animal." As a phototropic reaction, they then fly up to a wire-gauze "non-return" catching-box in the top through which daylight shines.

The "JV" Trap is closed below and the flies **climb up the outside** into the "non-return" catching cages, which are suspended like lifeboats on the "shoulders" of the trap. A wire gauze guard impedes the return downwards of flies that have passed it.

FIG. 3. Swynnerton's roller trap (with large drum), viewed from the back. The flies settling on the drum are carried up under the catching-box and are there brushed off and fly up into it. The gearing later evolved for this trap is shown in pl. 10, fig. 4. This gearing ensures an easy start and slow revolution. This trap is useful for *G. morsitans* and *G. swynnertoni* which refuse to enter other traps in sufficient numbers.

FIG. 4. Bax's "moving staircase" trap (BSR), with two cylinders round which the whole screen climbs like a "caterpillar" track or a roller towel, shown in an open space in *morsitans* country, at Kazikazi. The flies are carried in as in the case of the drum traps. As in fig. 3 and pl. 8, fig. 4, the tail vane keeps the trap always head on to the wind, suspension being from a bicycle hub which serves as a swivel.



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Screens and traps for the capture of tsetse flies.

Plate 8.

Five traps for the capture of tsetse flies.

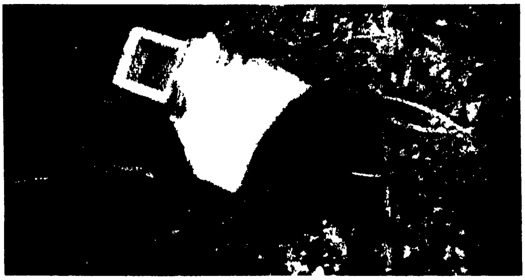
Fig. 1. The Electric Trap, attached to the tailboard of the lorry in an experiment carried out in Utete. The oil tray below is shown into which the flies fall on receiving the shock which results from their touching two of the wires and so producing a contact—for the wires are charged alternately negatively and positively. Numbers of *G. brevipalpis* as well as of the smaller tsetses were trapped thus.

Fig. 2. The "SV" Trap for use with large animals as bait. The flies climb up the outside into the catching cages on the shoulders of the trap. They cannot enter the chamber in which the animal stands. An exceptionally successful trap, though the animal could not be seen by the flies.

Fig. 3. A simple development from our screens (pl. 7, fig. 1, and pl. 10, fig. 2). Awning screen traps (AS, formerly SS) with (*a*) gauze "buttocks," (*b*) hessian "buttocks" (both ASB), and none. The flies climb up the screens, being attracted to go even higher by attractive colours and textures arranged above those that are less so. This trap is very effective (and used extensively) for *G. pallidipes* and *G. palpalis*, but not for *G. morsitans* or *G. swynnertoni*.

Fig. 4. Narrow Roller Trap. The grey strip attached to this trap had faded. It should be dark. The success of this trap depends on the flies climbing the screen and settling on the narrow black drum, which, revolving, carries them into the catching cage along the top, as in the trap in pl. 7, fig. 3. The gearing shown in pl. 16, fig. 5, is necessary.

Fig. 5. The Cavern Trap. A crinoline trap laid or suspended on its side, as shown here. Note the black inside lining. The idea here is that the trap represents to the flies a breeding-place.



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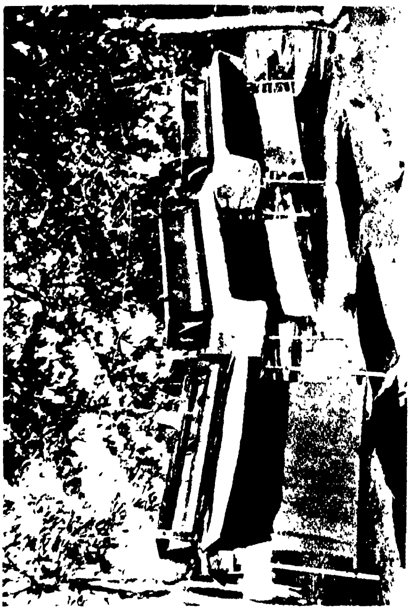

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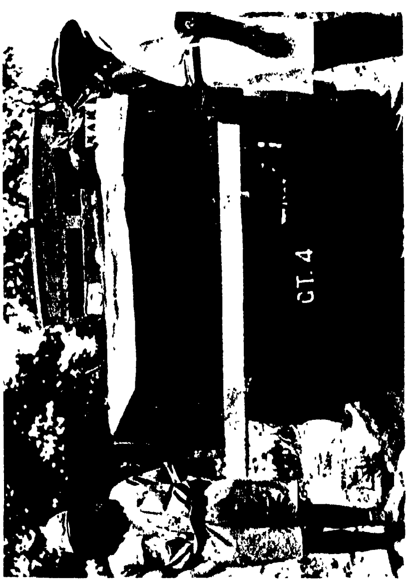

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Five traps for the capture of tsetse flies.

Plate 9

Four traps for the capture of tsetse flies.

Fig. 1. The rotary apparatus used to make Chorley's crinoline traps revolve. The " AS " (or " SS ") screen-traps (pl. 2, fig. 3) can be made to revolve otherwise also, as Blunt showed, by making the lower part of the screen **S**-shaped in section.

Fig. 2. Chorley's Narrow Crinoline Trap for tsetse flies, useful for *G. palpalis*, if skilfully sited. The " skirt " hangs straight down like a trouser-leg. The most usual form of catching cage for tsetse crinoline traps is shown, as is the rotary apparatus of four diagonally-bisected petrol tins dependent from horizontal rods in the form of a cross and catching the wind like anemometer cups. The trap is shown set in a good position : the fly movements are along the border of this barrier of dense bush.

Fig. 3. Chorley's Crinoline Trap (broad form with jar). The bottom of the jar, if a jar be used, should be fitted with a removable, " non-return," wire-gauze cone, as shown here. A rotary cross, placed as indicated by the wooden rod, may be added (*see* fig. 1). Vertical or diagonal markings of white or another colour may be painted on the outside of the " crinoline " to give the impression of progressive movement as the whole trap revolves. The dark swollen rim below is believed to be an attraction to the mouth of the trap.

Fig. 4. " Tent " Trap. A hidden and protected calf formed the bait in the trap on the right and there was no animal in the control on the left; photographed on the day on which the trap with the calf took 584 tsetse flies (mainly *G. pallidipes*) in $5\frac{3}{4}$ hours during the morning. This photograph and that shown on pl. 7, fig. 2, together give a nearly complete picture of a small natural open space in the bush (" feeding-ground 2 "), with a path (not shown) running through and a riverine thicket on its west, which produced great numbers of *G. pallidipes*, the largest catch therein in the traps being 1,200 flies in one day, though the flies appeared very little to man.

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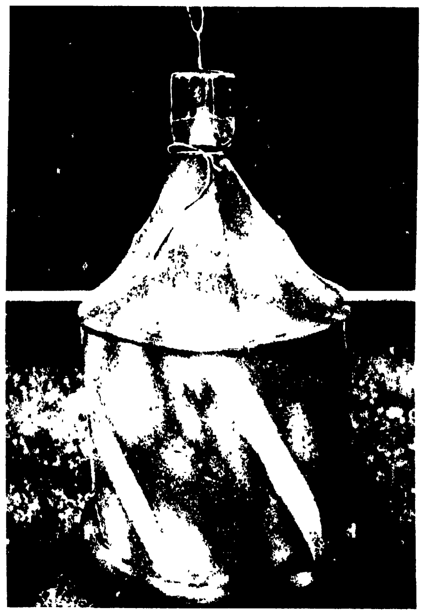

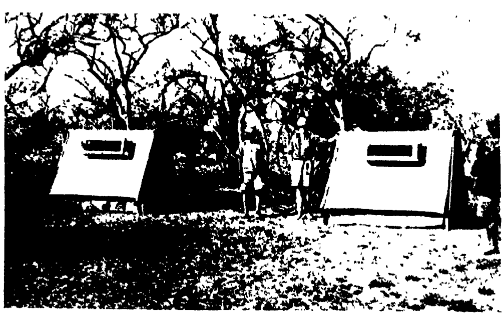

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Four traps for the capture of tsetse flies.

Plate 10.

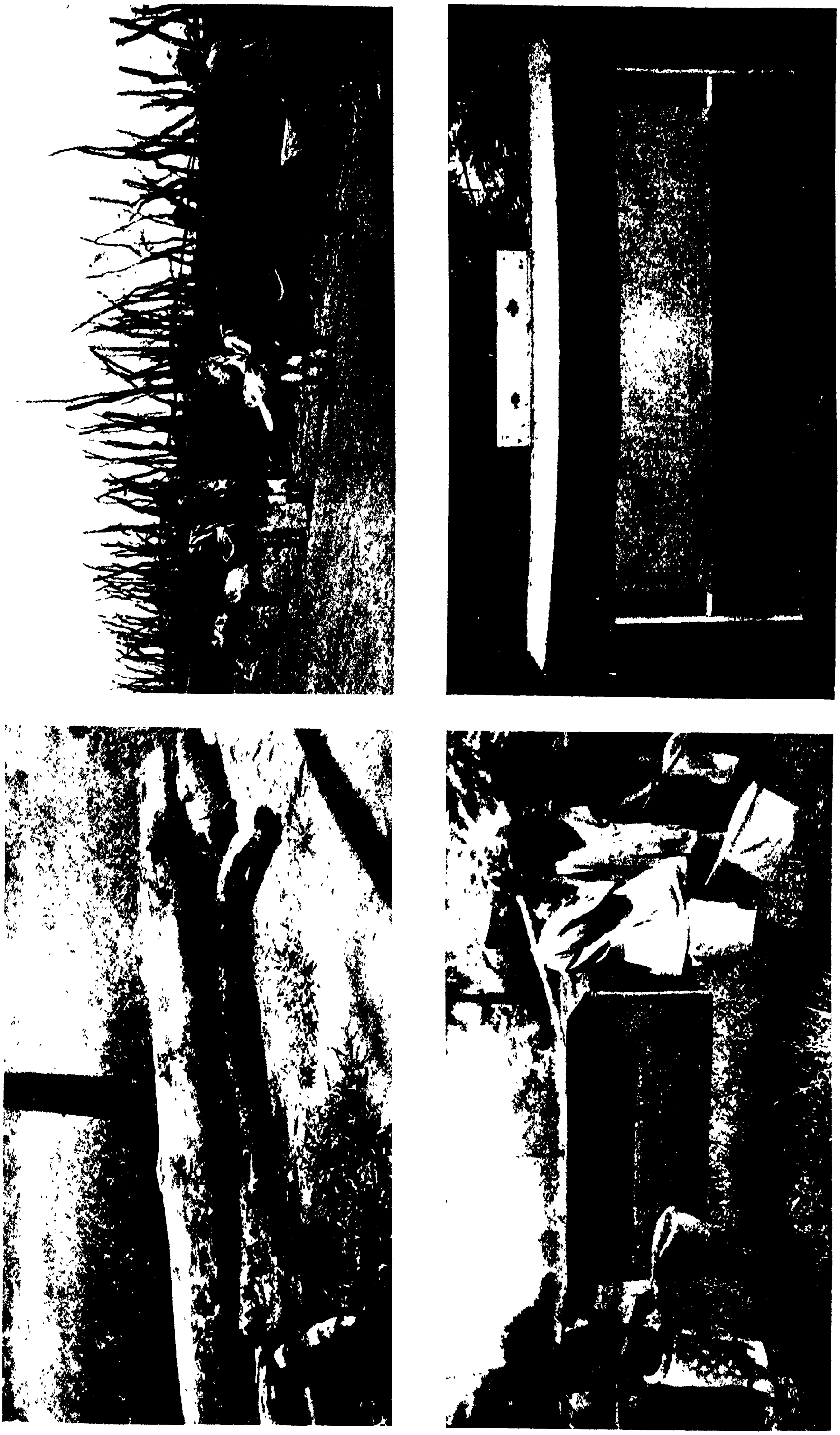
Screens and traps for the capture of tsetse flies.

Fig. 1. Nash's improvement of Lamborn's log trap. Note the bark "curtains" and the rollers. The flies drop their larvae under these logs and these turn quickly to pupae. The rolling back of the log on its rollers leads to the exposure to the sun of the ground containing the pupae and the killing thereby of the latter. Natives go round turning the logs every three weeks, the minimal effective pupal period just exceeding this. This trap is promising against *G. morsitans* at Kikore, quite unpromising against *G. swynnertoni* at Shinyanga.

Fig. 2. The "T" hand-catching screen, representing the form of screen always now used if possible. Screens (preferably dark grey) are very attractive to the female flies. *See* pl. 7, fig. 1 (explanation).

Fig. 3. Small boys sallying out with plain screens for the daily attack on the flies in the concentration grounds of *G. swynnertoni* in a block of ground, "5A," in Shinyanga, measuring 13 square miles. A very great reduction in the fly population was brought about in a year, but not extermination.

Fig. 4. The "awning screen trap" (ASC). For cheapness, the catching cage on the top is limited to a small box, and the black and grey strips on the screen are arranged as "directive markings" concentrically from the centre outwards.



Screens and traps for the capture of tsetse flies.

PLATE 11.

The advancement of the vegetational succession *in the miombo* by not burning the grass.

Experimentation in miombo wooding at Itundwe (see centre of map 1) *in the advancement of the vegetational succession towards its dense climax type by not burning the grass ; and the effect of this on* G. morsitans.

FIG. 1. The wooding thickened by the up-growth of (chiefly) a woody *Indigofera* (*I. gyrocarpa*) and tree-saplings, as the result of five years without grass fires. Season of leaf-fall. Visibility very shallow, flies greatly reduced in numbers, breeding much reduced.

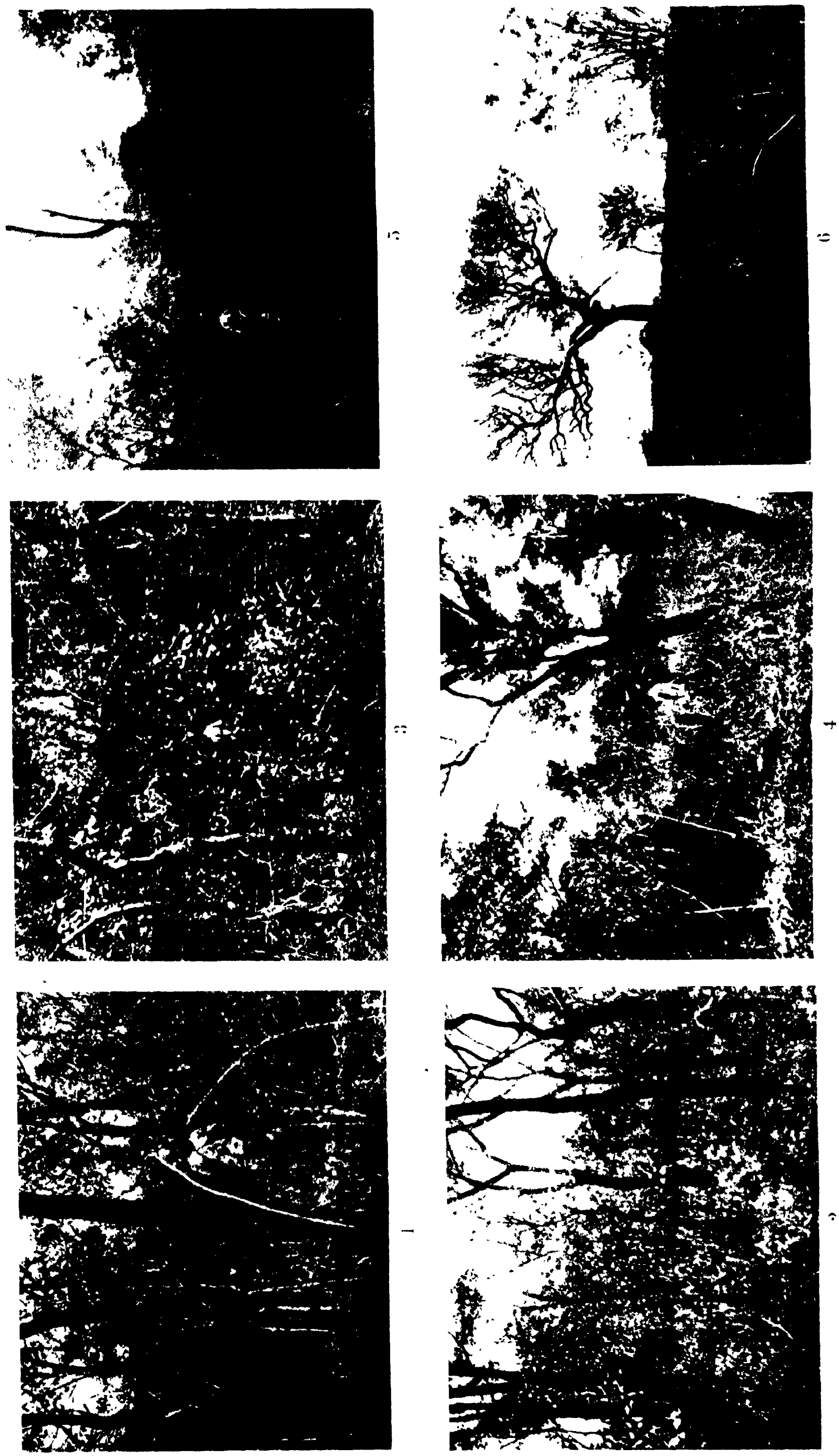
FIG. 2. Area immediately beside that shown in fig. 1, but, in the control area, burned annually in normal fashion. *Indigofera*, etc., present, but no up-growth. Maximum visibility between trees 240 yards. Flies abundant and breeding progressing apace.

FIG. 3. The strongest densification in the area kept unburned at Itundwe; much *Acalypha* forming dense thicket.

FIG. 4. Area immediately beside that shown in fig. 3 on ground annually burned. Much-burned thicket of *Acalypha* on the left.

FIG. 5. An experiment in felling all bush (miombo) and then keeping out grass fires. Regeneration after five years of fire exclusion.

FIG. 6. In the control to the area shown in fig. 5. Trees and shrubs, except a large *Ostryoderris Stuhlmannii*, felled; the area then burned normally annually. The contrast should again be noted.



The advancement of the vegetational succession *in the miombo* by not burning the grass. Paired photographs above, unburned; below, the burned control.

Plate 12.

Indirect attack by isolating certain types of woodland.

Fig. 1. The exact site, then open grass-land with trees, of which a photograph is given in pl. 5, fig. 8 of the annual report of the Tsetse Research Department, Tanganyika Territory. It is situated on the edge of the now four years' unburnt Block 4A. The tree showing the native's cap is that which shows behind it in the annual report for 1930. The keeping of this block unburned has not only produced an immense drop in fly numbers (*G. swynnertoni*), but (showing its value as a measure of game management) is resulting in a marked qualitative change in the game population.

Fig. 2. The exact site of which an account is given on p. 272 above. This thicket strip, 300 yards wide, while not 100% effective, is proving of great value for protection from infestation by *G. swynnertoni* of a road that was always well infested before the thicket grew up. It grew up as the result of the exclusion of the annual grass fires.

Fig. 3. The south-east corner of the great Huruhuru plain system. The various grasses, representing differential soil conditions, especially that of moisture, are well seen on the left—a further illustration of the value of air survey—as are the aerial landing strip, Stiebel's dam just above it, and the south-eastern corner of the very extensive woodlands of gall-acacia which occupy much of these plains and which since these photographs were taken have been further separated from the fly bush by clearing, and thereby have been cleared of tsetse fly. Part of the fly belt proper is seen dark in the distance.

Elimination of tsetse by means of " isolating " barriers, cleared, or of thicket, will be applicable to any type of country, which the species of tsetse concerned does not use all the year round.

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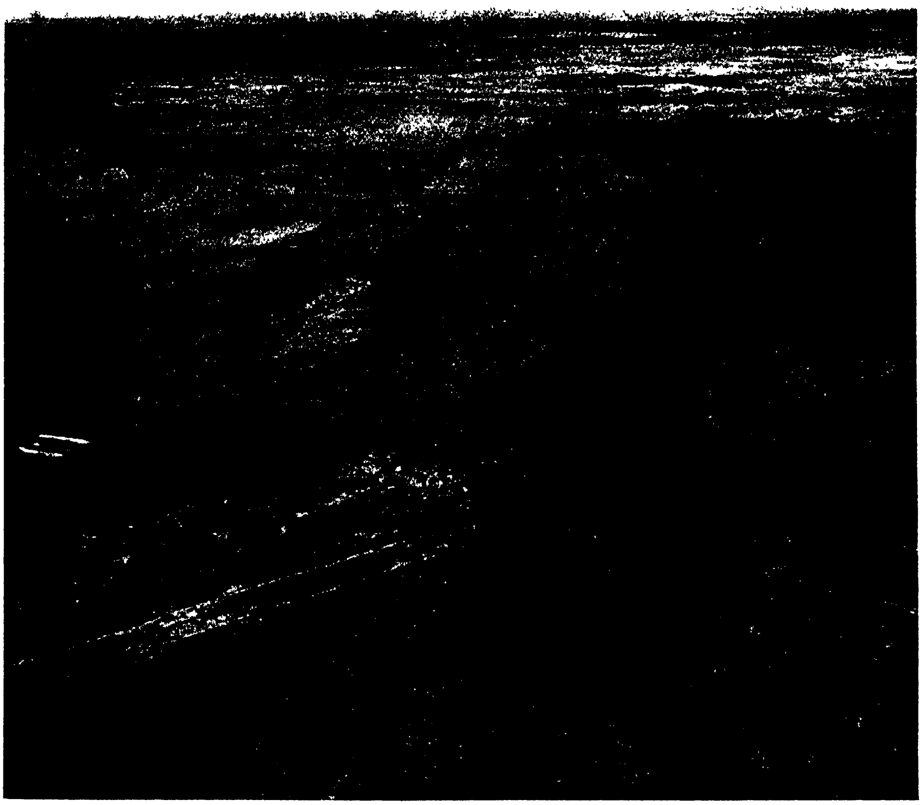

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Figs. 1–2, the advancement of the succession on eluvium *in the dry thorn-bush* (p. 272); fig. 3, reclamation by isolation: the Huruhuru Plains (pp. 385–393). Gall-acacia wooding (right mid-distance) and the exclusion there of the flies.

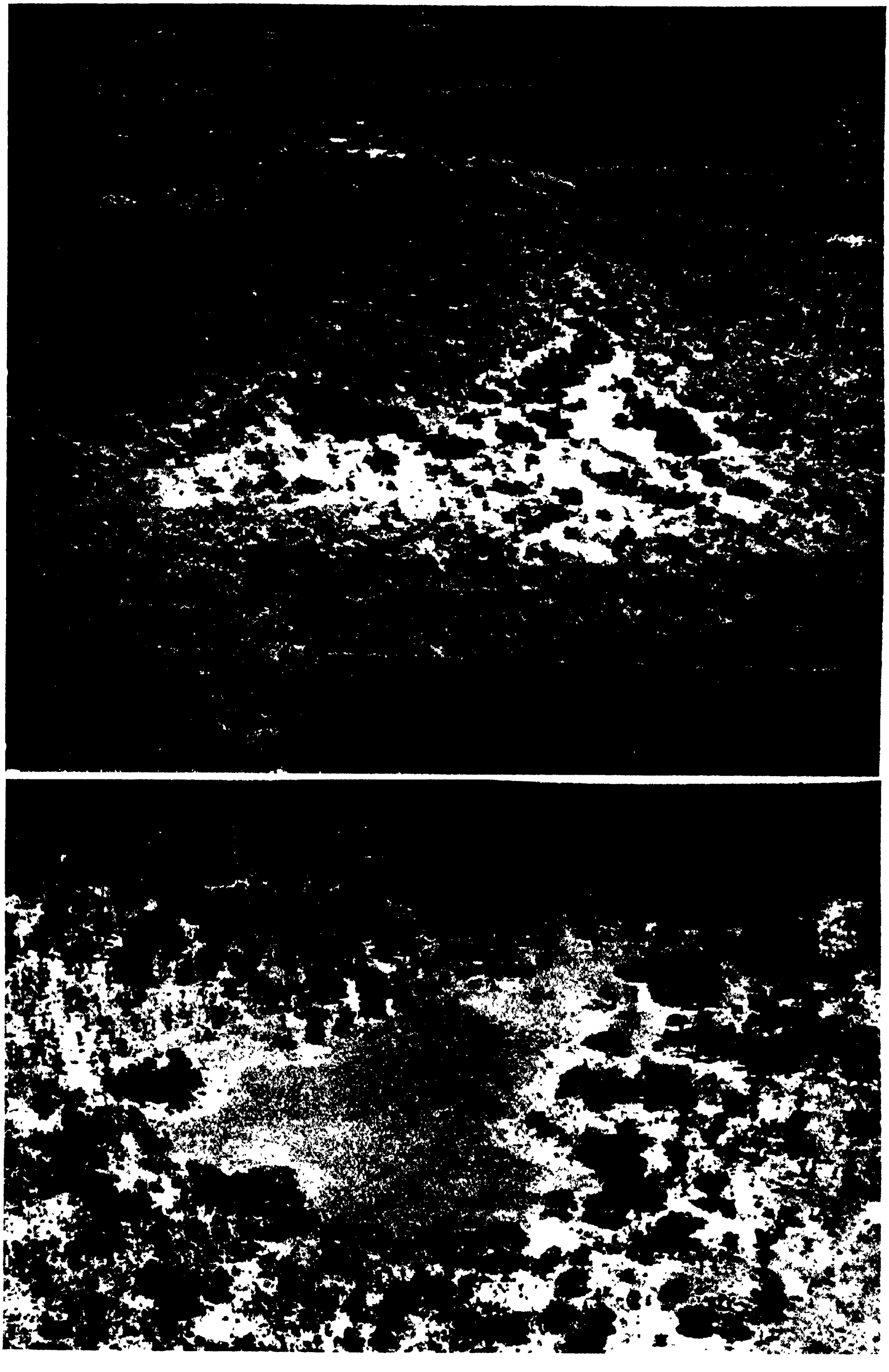
PLATE 13.

The vegetational requirements of *G. swynnertoni* and the opportunity which they offer for attack at relatively small cost.

FIG. 1. An oblique aerial photograph of *Ostryoderris–Commiphora-Fischeri* wooding on eluvial ground and of hard-pan drainage lines interspersing it in Block 5A, Shinyanga. The former is rest-haunt and the latter is combined home and feeding-ground for *G. swynnertoni*. When these flies become fairly scarce through any of the measures, they concentrate and range in the hard-pan strips, using the thickets in these as home and the open ground still as feeding-ground, so that the sexes meet up to the last. It was at these concentration grounds that the catching off screens in Block 5A was conducted (*see* pl. 10, fig. 3, and its explanation). It was the clearing of these concentration sites only that ultimately expelled the flies from Block 5A and the " Outer Circle." Most of the wooding is leafless and the presence of leafless *C. Fischeri* is represented in mid distance by a grey misty appearance.

FIG. 2. A black-soil alluvial " mbuga " with hard-pan and eluvial adjoining. These completely open mbugas are feeding-grounds only, the eluvial a home only, the hard-pan often both.

Both these photographs illustrate the indispensability of air reconnaissance for the detection of fly-concentration grounds (many of which would otherwise be missed) where the measure may take the form of an attack of some kind on these foci.



The vegetational requirements of *G. swynnertoni* and the opportunity which they offer for attack at relatively small cost.

Plate 14.

Direct and indirect attack combined.

Fig. 1. The Ndama stream and part of Block 5B in Shinyanga. Organised grass burning (direct and indirect attack) and discriminative clearing (indirect attack by control of cover) are applicable here, since the grass is generally good and the sites to be cleared are limited. Discriminative clearing consists in clearing the minimal amount of vegetation in limited sites indispensable to the flies at some one season of the year.

Fig. 2. Direct attack (by the driving effect of a fire) and indirect attack by increasing desiccation and setting back the vegetational succession to a stage unsuited to the tsetse (here *G. swynnertoni*)—thus making the vegetation too thin and also destroying the breeding-thickets. *Acacia Benthamii* and *A. spirocarpa* trees killed by late organised grass fires, and thickets burnt out. This site is near Chibe, the old tribal headquarters, Shinyanga, which was reclaimed by this means. Only *Acacia* wooding is affected as strongly as this.

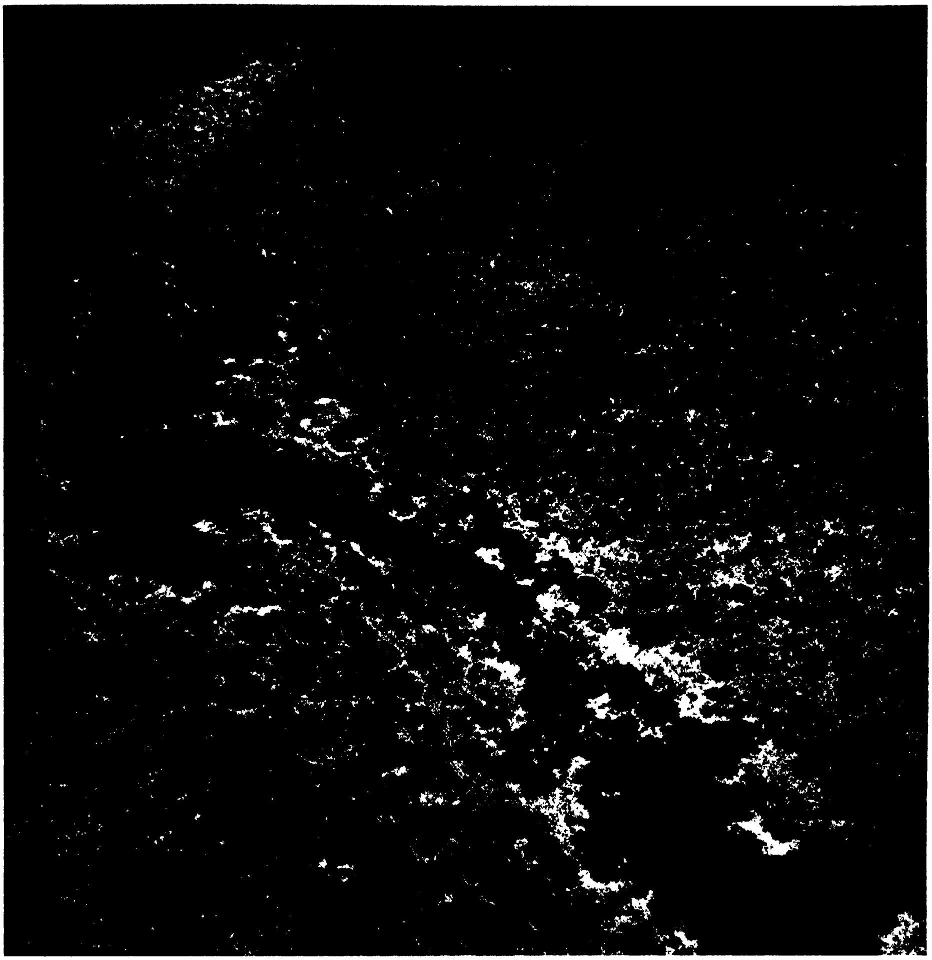


Fig. 1, country suited (*a*) to organised grass burning, and (*b*) to discriminative clearing in the dry thorn-bush with a gallery (riverine) thicket; fig. 2, the effect of late organised grass burning on certain acacias and small thickets, and thereby on the tsetse population.

PLATE 15.

A feeding-ground of *G. swynnertoni*, and a reclaimed area in process of settlement.

FIG. 1. A feeding-ground site of *G. swynnertoni* from ground-level after a grass fire.

FIG. 2. After reclamation, settlement. The natives are gradually occupying an area (Blocks 2 and 3, Shinyanga) as the result of its first having been cleared of tsetse by organised grass burning without clearing of bush. The type of settlement that ultimately cuts down every tree and becomes over-grazed and eroded is what the Tsetse Research Department are trying to avoid.

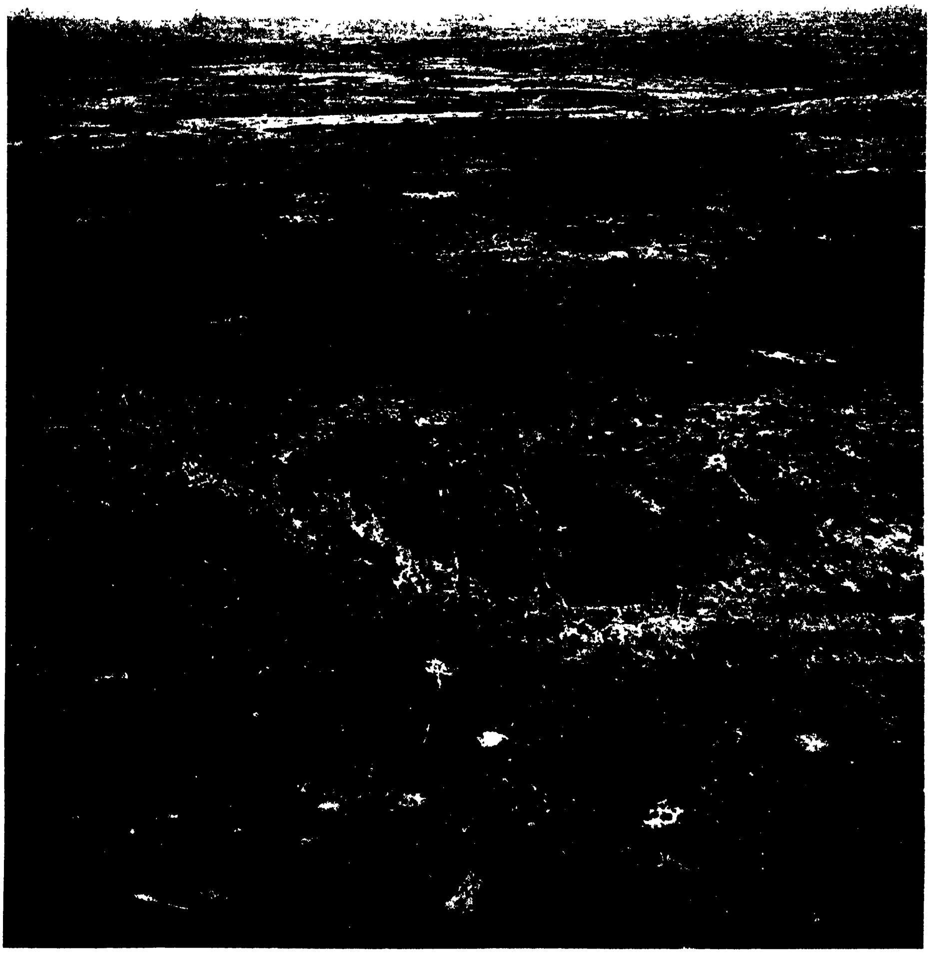


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Fig. 1, a drainage glade in the dry thorn-bush, a feeding-ground for *G. swynnertoni*; fig. 2, occupation by natives of an area reclaimed from tsetse flies.

PLATE 16.

The provision of water for the settlers; and the gearing of the roller traps.

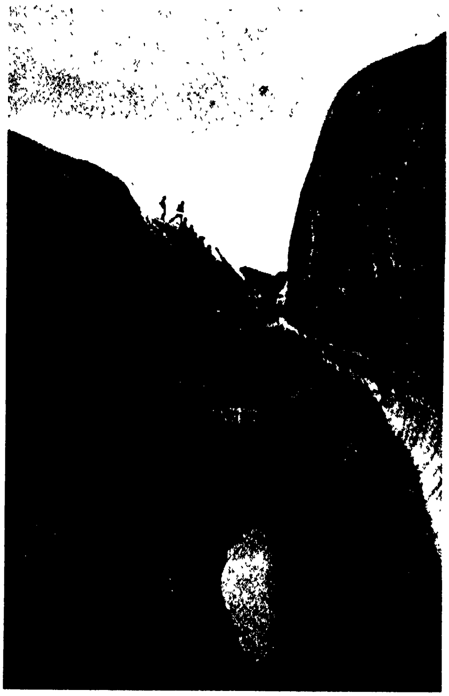
FIG. 1. The Sayu tank, Huruhuru, Shinyanga (one section only). The long bank opposite is one of two which, converging on the tanks, guide in the rain water from the very slight slope. They can, in addition, hold up between them a large sheet of water over and above what the tanks hold. These tanks are provided in impermeable soil for the use of native settlers and their cattle in the areas reclaimed.

FIG. 2. Conserving the run-off from great rocks; Ndode, near Chibe, Shinyanga. Present capacity 200,000 gallons, potential capacity nearer 800,000. The water is guided in at the ends by cement walls a few inches high which encircle the whole great rock. Here there happened to be a natural rock reservoir, full of earth which was removed. Normally a reservoir would be dug at the foot of a great rock and the water be guided into it as described.

FIG. 3. A coffer-dam made (most successfully) in the bed of a small sand-stream near Lubaga, Shinyanga, in 1925. The underground dry-season flow of water is held up by the wall which is based on a clay-bed below, and hardly projects above the sand. Collecting above this, the water filters out of the sand through holes in the sides of the well-like masonry sump. From this, or from holes dug in the sand, the water is drawn.

FIG. 4. The game tank in Block 4B, Shinyanga. Much used already by game animals and lasting out well the dry season. A feature of the other game sanctuaries also, in Blocks 10A and 10C.

FIG. 5. Double bicycle-chain gearing for "roller" traps (pl. 7, figs. 3 and 4, and pl. 8, fig. 2), making them start very easily and turn very slowly. The former is necessary when the wind is very light, the latter is found to be necessary not to deter the flies from settling.



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Figs. 1–4, the provision of water in areas reclaimed; fig. 5, the gearing of the roller traps.

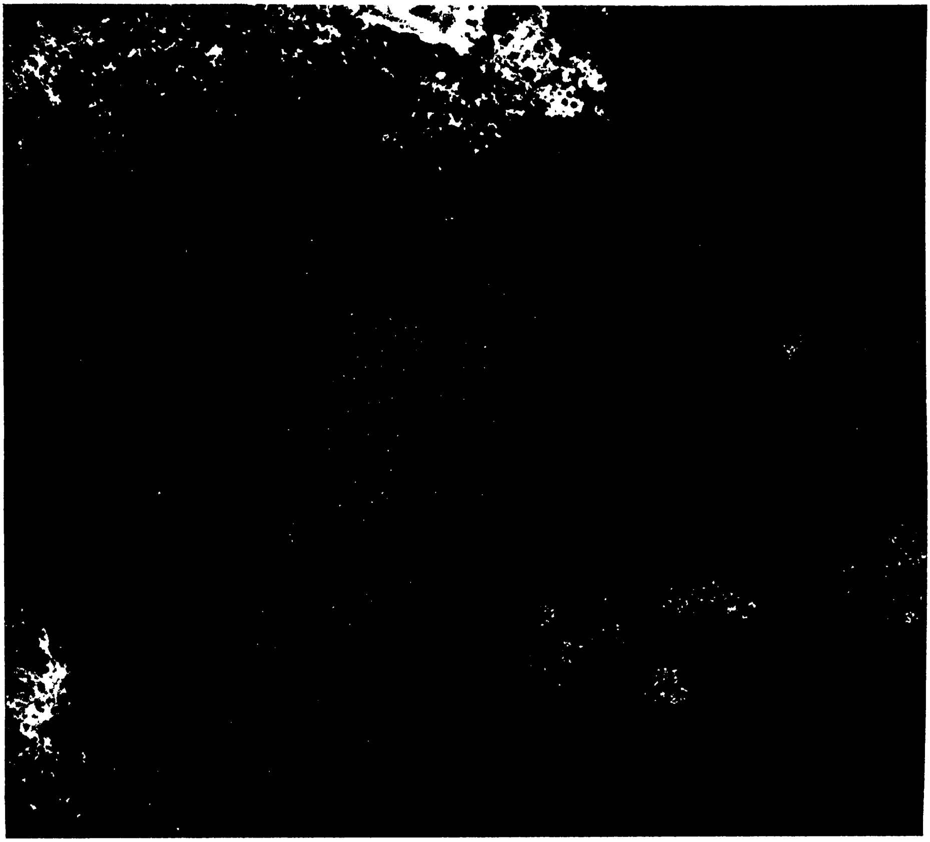
Plate 17.

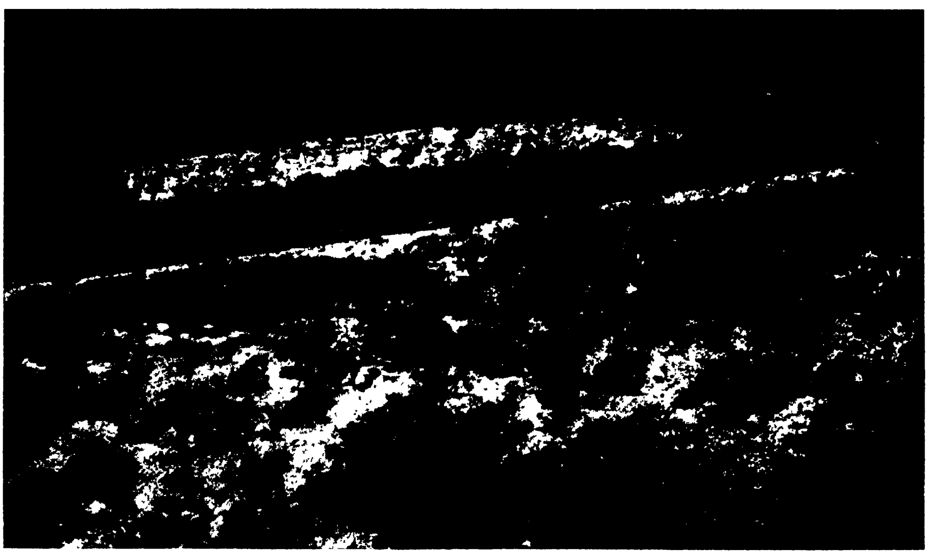
Unbroken thicket as a barrier to the passage of tsetse flies.

Fig. 1. Vertical aerial photograph of a small part of the thicket at Kazikazi, " Itigi " (*Burttia–Baphia*) type, for which see the map on pl. 20, fig. 2, and map 6. Two arms of the enclosed " island " of savanna (Mgumu " island "—*see* pl. 20) show on the left. An elephant path descends from the lower arm. The thicket generally is leafless and the light-coloured patches represent groves of *Craibea Burttii* in leaf.

Fig. 2. Oblique aerial photograph of one of Burtt's semi-clearings in the Ulimiri thicket (*see* fig. 1), unfinished, 50 yards in : leafless season. The clearing is thinned to the point of representing savanna wooding attractive to the flies, and a brush game fence erected all round for the exclusion of game is visible. The thicket projections lying between the 50 yards' thicket strip and the camera were thinned to savanna density after the photographs were taken. The savanna wooding in the foreground carried a high density of *G. morsitans*. The object of the experiments was to see to what distance the flies would penetrate the thicket when in leaf and when leafless.

Other similar clearings were made 100 yards in, 400 yards in and 900 yards in, and interesting differential results were obtained, as described on pp. 309–311, and shown in fig. 21.





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Unbroken thicket as a barrier to the passage of tsetse flies (pp. 307–315). Fig. 1, vertical aerial photograph of part of the great Itigi thicket; fig. 2, oblique aerial photograph of the site of one of the experiments carried out by B. D. Burtt in regard to the distance to which flies will penetrate unbroken thicket.

Plate 18.

A cleared strip as a barrier to tsetse fly; and an area suffering from the first stage in erosion.

Fig. 1. A too narrow but otherwise typical clearing at Shinyanga separating Block 11 (right—a non-burning experiment) from Block 5A (left—cleared of tsetses by late organised burning and, later, discriminative clearing). Block 5B (for discriminative clearing only) is seen on the left in the distance beyond another clearing. The experimental game fence of *Commiphora* is seen lining the Mwantine road on the right and beyond may be seen the fences, on the left of the clearing and also crossing it, which formed the experimental "barrier" 3 miles long and 800 yards broad, across which the fly crossing experiments took place, game and man being excluded. These proved this clearing to be too narrow to form a fly barrier.

Fig. 2. The first stage in erosion. Typical cultivation steppe in Shinyanga, cultivated closely on wrong lines and heavily over-grazed. The natives leave only baobabs and tamarinds unfelled and the grass is destroyed each year completely by the cattle. This bares the ground before the first heavy rains, the thunder winds preceding each storm fill the air with earth up to several hundred feet, which is carried off into the tsetse bush, and wash does its share of the havoc.

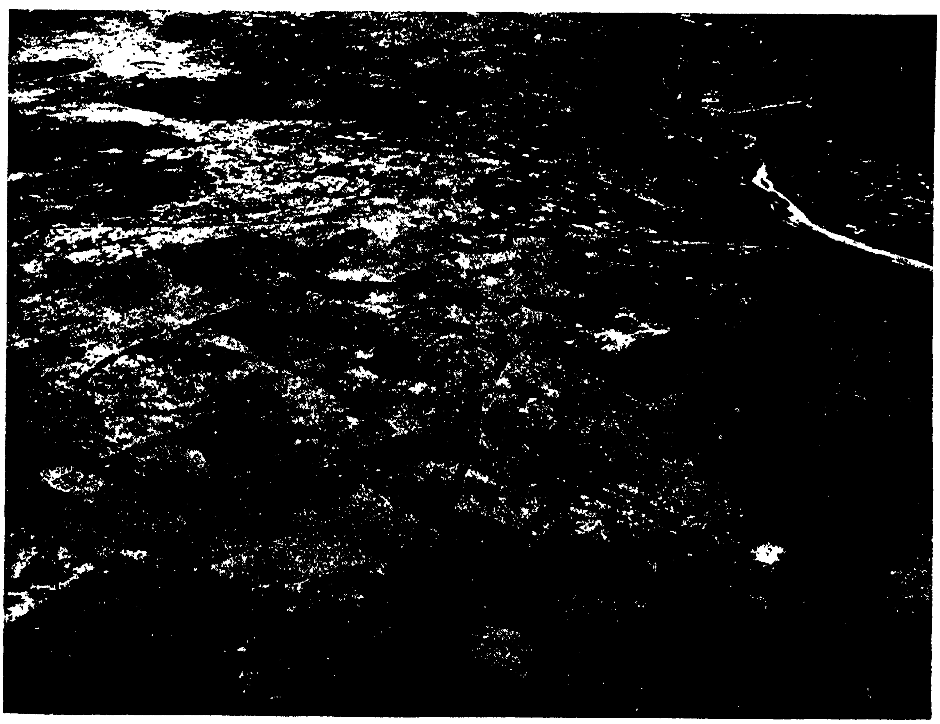
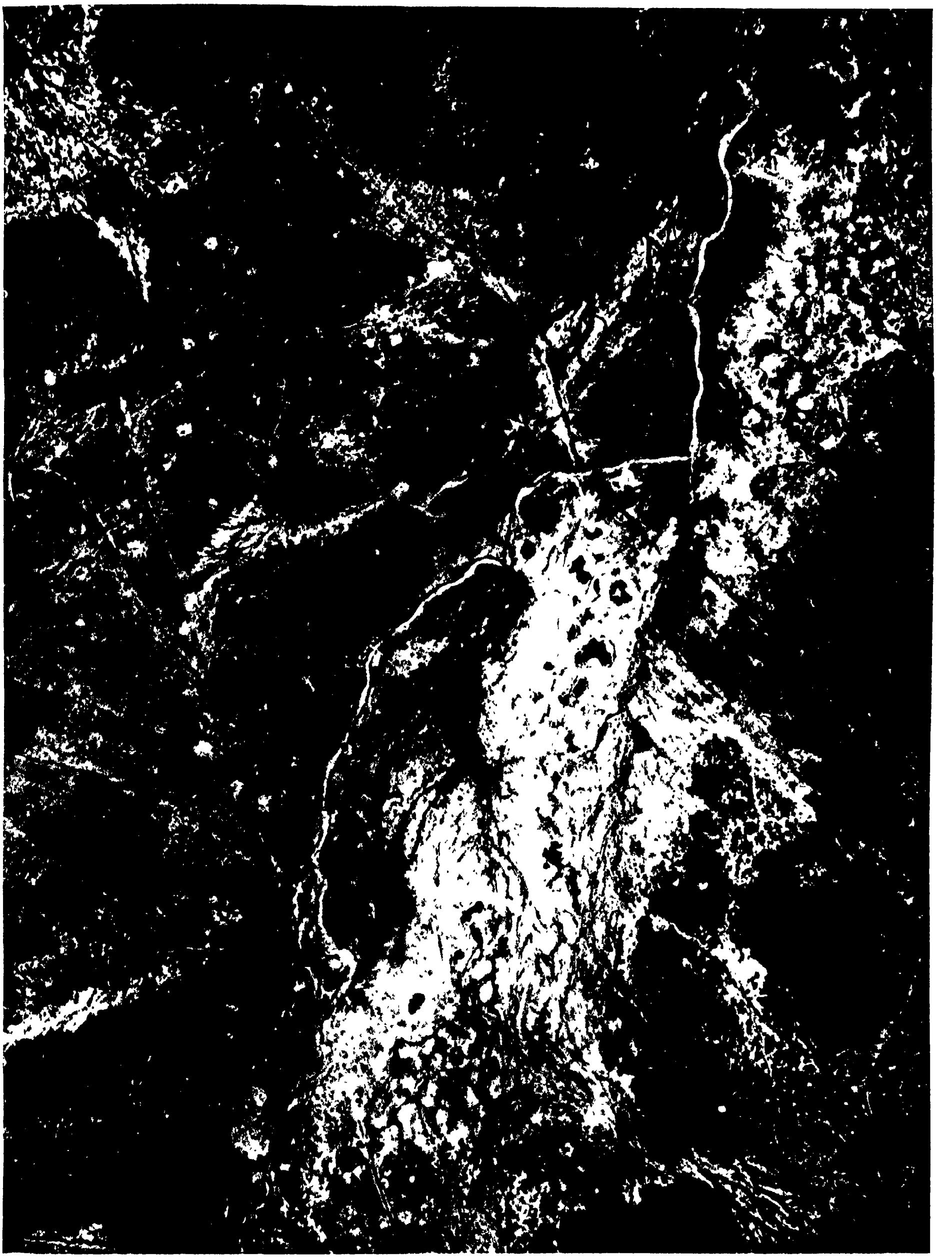


Fig. 1, one of the clearings used for isolating blocks of fly bush which it is desired to attack (*see* map 2); fig. 2, cultivation steppe, over-grazed (stage 1 in erosion).

PLATE 19.

The second stage in erosion.

A vertical aerial photograph of over-grazed cultivation steppe in Shinyanga, going fast to erosion. The branching and re-branching channels resemble an arterial chart.



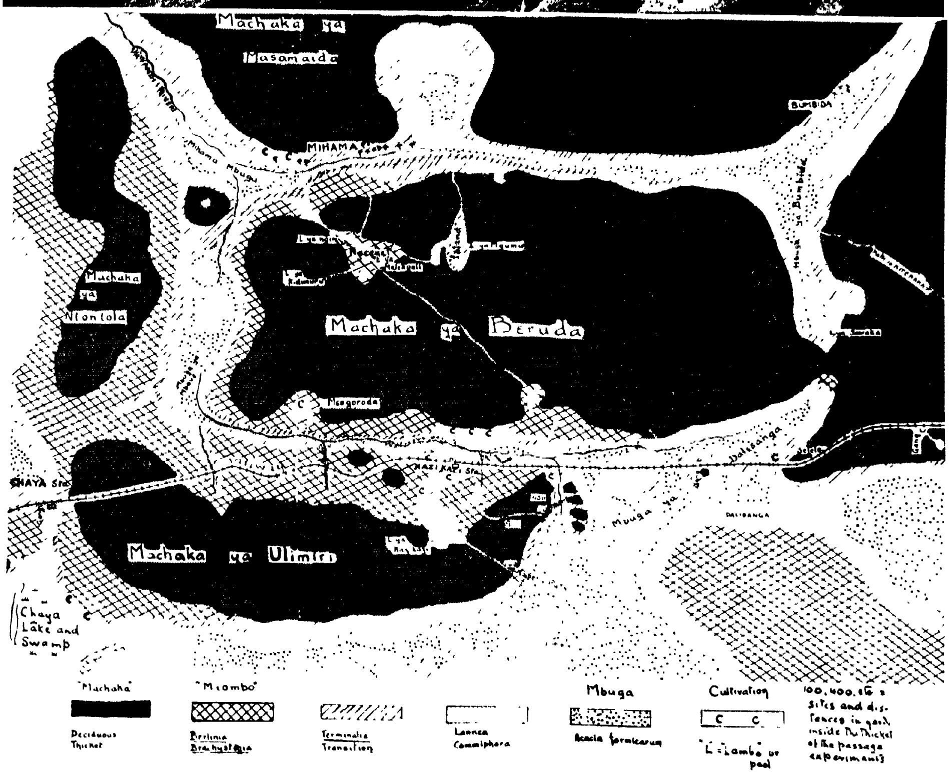
The second stage in erosion ; a vertical air photograph showing erosion, " donga," and " sheet."

Plate 20.

The third stage in erosion; and a vegetation map of Kazikazi.

Fig. 1. The third stage in erosion, caused by over-grazing, and typical of considerable pieces of country. Photograph by Dr. D. R. Grantham in the Central Province, Tanganyika.

Fig. 2. Vegetation map of Kazikazi, made by Burtt from sketches and notes made in the air. The sites of his thicket experiments (pl. 17, fig. 2) may be seen here, including the Kapetu path and (on right, below L. ya Swaka), the "thicket neck." It was from the air that these sites were selected. They could not in this level country have been found on the ground short of weeks of reconnaissance. The very great value of a mere sketch reconnaissance by a botanical expert knowing the trees is shown also. *See* pp. 307–315.



1

2

Fig. 1, accelerated erosion well advanced (stage 3); fig. 2, vegetation map of Kazikazi (pp. 307-315) compiled from aerial sketches and notes.

Plate 21.

The hunger stages of tsetse flies; and methods of marking flies.

(*a*) The hunger stages of tsetse flies (Stages 1–4). The four hunger stages of the tsetse flies, for the details of which *see* pp. 39 and 40. By taking the average of these in the flies anywhere captured, it can be ascertained whether they are suffering distress either as the result of the measures taken or otherwise; this may influence the measures adopted. Weather conditions influence hunger much more than does scarcity or abundance of game animals. Right-hand downward row shown through transmitted light, remainder by reflected light. The pale areas in the right-hand row represent translucence. Stage 1 can be fuller and stage 4 can become thinner than shown. The hunger stages have been duly correlated with the internal condition of the flies.

(*b*) Diagrams showing differences between *G. morsitans* and *G. swynnertoni*. **A**—abdomen pattern of *G. morsitans*. **B**—abdomen pattern of *G. swynnertoni*. The pale parts of the former are usually of a fairly bright fawn colour, those of *G. swynnertoni* are greyish, usually with a slight fawn tinge down the median line of the abdomen. The greater relative width of the abdominal segments of *G. morsitans* should be noted.

(*c*) Methods of marking flies. The centre (grasshopper) figure, no. 3, shows the whole " clock " which can also have an inner row as in fig. 2. " 2 " in fig. 3 represents the remarking of a recapture on a Sunday. In *circle* " 3 " can be placed the colour for the week: if a combination of two colours is used many weeks can be recorded. The seven " ones " thence round clockwise represent the days of the week – Sunday, Monday, Tuesday, Wednesday, Thursday, Friday, Saturday, counting clockwise. The central spaces are reserved for other information, as place and hunger-stage.

In the other figures **R** is red, **Br** is brown, **Y** is yellow, **W** is white, but any colours or colour-combinations can be used.

In Scott's system (fig. 2) are shown place, date, and time of day by the colours in positions 1 to 5. The condition of the fly, when marked, is shown by an additional colour on the periphery at 8, 9, and two corresponding positions (6, 7) on the opposite side.

Day of week is shown by colour at position 1 or 2.

Time of day is shown by position of the above colour—1 for morning and 2 for afternoon.

Place (station at which caught) is shown by colour at 5.

Week (in series of 7 weeks) is shown by colour at 3. Number of 7-week series is shown by colour at 4.

Condition of fly—hunger, whether young or old—is shown by position of the peripheral mark or marks at 8, 9, or the corresponding opposite positions 6, 7.

The colour used for the peripheral marks is changed at the end of every cycle of 7×7 weeks, thus allowing for $49 \times 7 = 343$ weeks without repetition.

In Jackson's system (fig. 1) only 2 colours are used on any day.

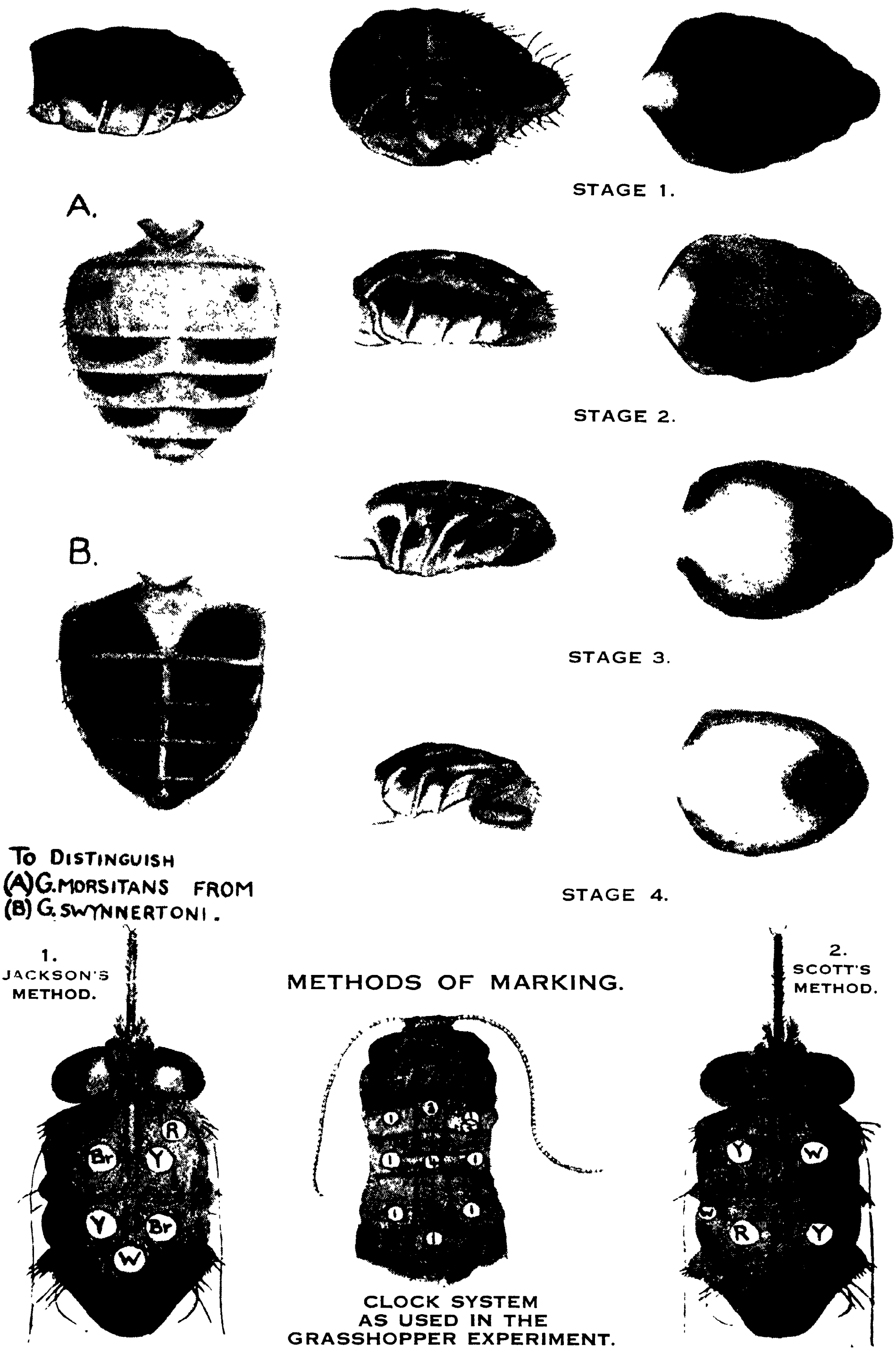
Date is shown by the 2-colour combination used.

Place of marking and condition of fly are shown by from two to four spots of the colours for the day arranged in the centre of the thorax according to some simple code devised for any particular experiment.

Particulars on recapture. Flies are re-marked with the pair of colours of the day, thus showing the date of recapture. These colours are placed on the periphery. Their placing is quite arbitrary, except that no two flies with identical original markings are given identical re-marks. For convenience of record, one colour is regarded as the hour and the other as the minute hand of an imaginary clock, the face of which is the thorax of the fly. Thus if (as in fig. 1) the first colour of the pair is placed at 1 o'clock and the other at 6 o'clock, the re-mark would be recorded as 1.30.

On this system no re-marked fly has any duplicate in the experiment, and no further re-marking is required. All particulars on every recapture are therefore entered in the records, but need not be marked on the fly itself. In this way, all particulars of individual histories can be ascertained.

Scott's system has the advantage that it can be used for years without repetition; Jackson's system is suitable for single experiments lasting about 70 days where individual histories are required.



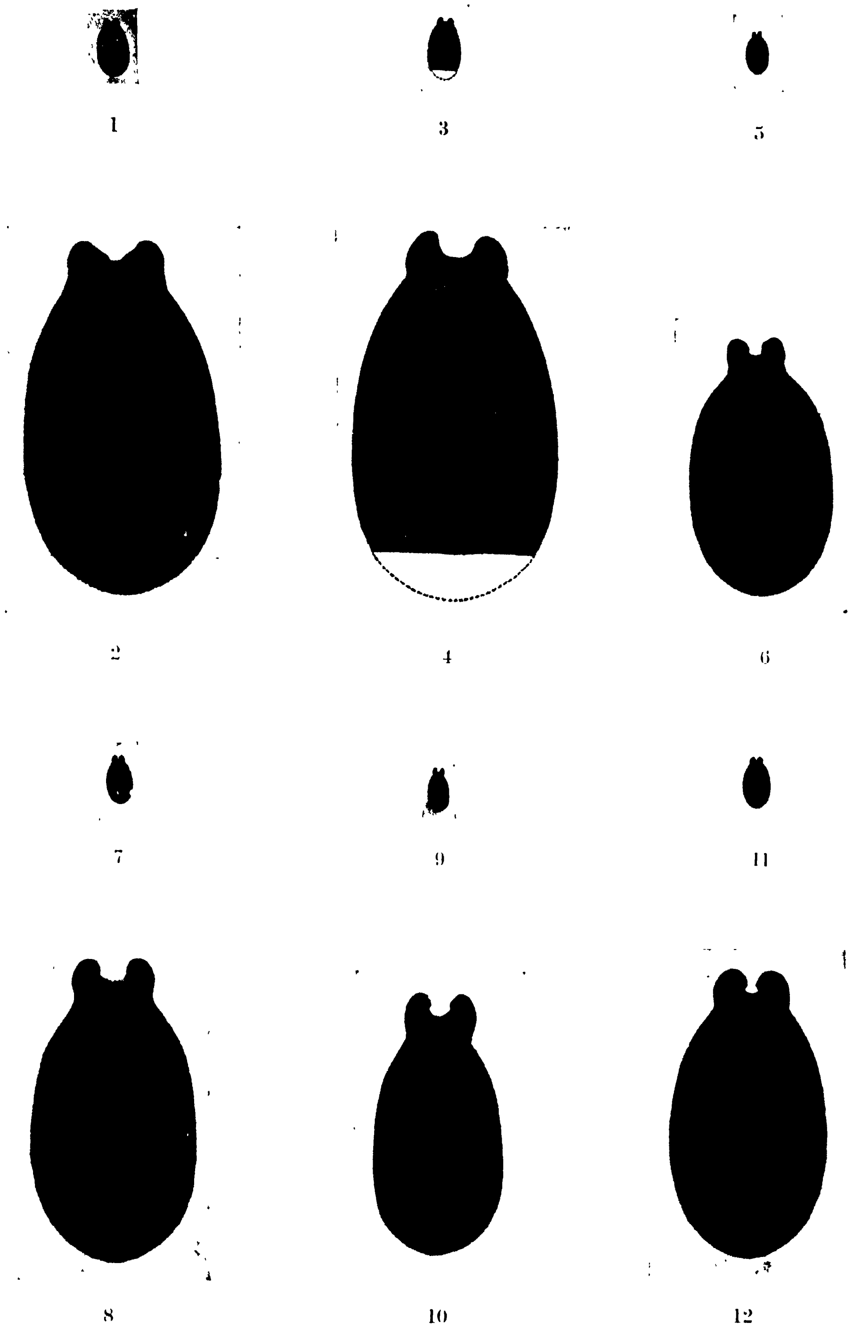
(*a*) The hunger stages (stages 1 to 4) of tsetse flies (9 figs.); (*b*) diagrams showing differences between *G. morsitans* and *G. swynnertoni* (2 figs.) (*see* appendix 10); (*c*) methods of marking flies (3 figs.).

PLATE 22.

Pupae of six east African species of the genus *Glossina* Wiedemann.

(Photographs of dorsal view.)

FIG. 1. *G. brevipalpis* Newstead, natural size.
2. ,, ,, enlarged six times.
3. *G. fusca* (Walker) (cephalic (lower) extremity missing), natural size.
4. ,, ,, ,, ,, ,, ,, enlarged six times.
5. *G. morsitans* Westwood, natural size.
6. ,, ,, enlarged six times.
7. *G. pallidipes* Austen, natural size.
8. ,, ,, enlarged six times.
9. *G. austeni* Newstead, natural size.
10. ,, ,, enlarged six times.
11. *G. palpalis* (Robineau-Desvoidy), natural size.
12. ,, ,, enlarged six times.



Pupae of six east African species of the genus *Glossina* Wiedemann.
(Photographs of dorsal view.)

Explanation of map 1.

The distribution of tsetse flies and (preliminarily) of the vegetation in Tanganyika and southern Kenya.

The explanation of the coloured symbols employed in this map is as follows :—

1. Miombo (*Isoberlinia–Brachystegia*–other-genera) infested with *G. morsitans*; in the east and north-west largely with *G. pallidipes* also, in the east with *G. brevipalpis* and *G. austeni*.
2. Miombo still uninfested.
3. Thorn-bush, more or less mesophytic, infested with *G. morsitans*, mainly *Acacia hebecladoides* in Bukoba-Ankole, *A. rovumae* in Wembere Plain, *A. pallens* from Kilosa towards Sadani. In this last and in South Bukoba, *G. pallidipes* also.
4. *Ostryoderris–Combretum Zeyheri–Acacia pallens* wooding with areas of *Acacia usambarensis Terminalia spinosa* and, elsewhere, of semi-evergreen broken thicket often associated with tall *Sterculia appendiculata*: a habitat for *G. morsitans* in Nzega, for *G. pallidipes* with local infiltrations by *G. morsitans* in the east, where also there is *G. brevipalpis* and *G. austeni*.
5. Communities (variously dominated) of *Protea* spp., *Faurea speciosa*, *Terminalis torulosa*, *Parinarium curatellaefolium*, *Sizygium awariense* and *Uapaca* spp. Largely infested with *G. morsitans*, though probably as an infiltration.
6. "Coastal debris." Plantations abandoned and others with remnants and regenerating patches of the original wooding and thicket. Flies *G. austeni*, *G. brevipalpis*, *G. pallidipes*.
7. Dry thorn-bush or nyika infested with *G. swynnertoni*, and (partially) with *G. pallidipes*.
8. Dry thorn-bush or nyika infested with *G. pallidipes* and, largely, *G. longipennis*. In places *G. brevipalpis*. On the Kenya coast, in thicket, *G. austeni* also occurs in numbers.
9. Uninfested dry thorn-bush or nyika.
10. Highland grass-country more or less open, varying from grass savanna above the miombo line to the tussocked alpine meadow of Kilimanjaro and to heath. Uninfested.
11. Lower grass-land with trees, not included in 10, due sometimes (as possibly in South Kavirondo) to past settlement, sometimes to swampiness. It might include also the grassy hill country, with scattered bamboo groves, of Kibondo, shown here under 10. Mostly uninfested, some small *pallidipes* belts, with *G. palpalis* on the streams, occurring west of Lake Victoria.
12. Climax closed-forest types, ranging from the mangroves of the sea-estuaries and the dense wooding of the lake shores to *Brachylaena*-forest (including plateau-forest, Nairobi), olive-forest, conifer-forest, and rain-forest (tropical, intermediate and temperate) and, under drier conditions, to the deciduous thicket areas of Itigi, shown in the centre of the map. Infestation by *G. austeni*, *G. brevipalpis*, and *G. pallidipes* occurs at the foot of the Usambara (Amani–Lushotoi). This is confined mainly to the edges and penetrates but little inside.
13. Open "Cultivation steppe," *i.e.* close native settlement. Uninfested except for the smallest patches. The small patches shown in the western *morsitans* belt are sleeping-sickness concentrations.
14. Vegetation unknown or areas lying outside region mapped.

The problems illustrated on this map are discussed on pp. 48–49, 58–61, and 85–90.

Explanation of map 2.

The tsetse campaign in western Shinyanga, Tanganyika Territory, and the experiments in progress, as they stood in 1934.

The map has been drawn in large part from aerial photographs, but Block 9 had not been surveyed at the time that these photographs were taken. Its eastern boundary is incorrectly shown on the map; actually the Block is wider in the north than in the south.

Block 10B, as shown here, is being divided in two portions in connection with the game experiments described on pp. 284–287, and its eastern half is being merged with Block 10C as a game sanctuary.

Discriminative clearing has been applied to Block 5B, and Block 11 is being used for an experiment in not burning the grass.

Reference should be made to Part 3, " Experimentation in attack " (pp. 241–296).

" Kizumbi Bay," cleared in 1924 and referred to on p. 260, is shown between Blocks 1 and 7. Lubaga, to which also reference is made in the present paper, is shown north of Block 1.

The Huruhuru Plains occupy the whole of the top left-hand corner of the map.

Explanation of map 3.

The tsetse campaign in the Lake Province, Tanganyika Territory.

This map gives an impression of the anti-tsetse campaign on the Lake Province of Tanganyika Territory. The importance of this map lies in the fact that it illustrates a comprehensive plan of campaign in a well-advanced stage, in which the country has already been divided into blocks of varying size and an ordered attack on the problem is in progress.

Reference should be made to Part 5, " Survey " (pp. 330–356) and Part 6, dealing with reclamation and settlement (pp. 357–423).

Notes.

1. Through, and to the right of, the words "Buhungukira Dodoma Block Scheme" (left centre of the map), vertical lines should be continued to connect the square hatching above with the horizontal lines below, thus indicating country reclaimed.
2. The word " Marialugu " (in the centre of the map, four inches from the top) should read " Marialuguru."

Explanation of map 4.

Vegetational map of the Kikore * District, Tanganyika Territory..

This map illustrates the primary vegetational survey described on p. 30. Reference should also be made to the study of eco-climates and physical factors undertaken by J. D. Scott, discussed on pp. 66–68 and in appendix 4.

* Spelt Kikori on the map.

Explanation of map 5.

The fly advances in the Western Kondoa and the Eastern Singida Districts, Tanganyika Territory.

This map shows the fly advance in Western Kondoa that was watched by Dr. C. H. N. Jackson for a long period (pp. 424–429). The lines show the fly front at successive periods, the last shown being that for 1932. The flies now (in 1936) are reported to be over the Rift wall to the west.

It should be noted :—

(*a*) that appreciable thickets have affected the advance, holding it up till they were outflanked;

(*b*) that between Kisima-cha-mungu and Masiliwa on the Kondoa–Irangi road, the advance did not follow the road and that, in fact, it failed to establish itself at that point (*i.e.* at the words "81 miles" on the map), the flies being merely carried thither by cars and pedestrians. It became established when it advanced south-westward from Dara.

The flies are reported now (1936) to have moved eastward across the road shown running south from Kondoa–Irangi.

Kandaga and Kikore, mentioned in the present paper, are shown in the top right corner of the map. Itundwe (referred to on p. 320) is just north-west of Mnenya.

Explanation of map 6.

The Singida fly advances.

This map has been prepared mainly from a map made by Mr. B. D. Burtt from sketches and notes made from the air.

The map illustrates :—

(*a*) the usefulness of the methods employed by Burtt for obtaining a vegetation map which, though topographically very rough, is of great use for tsetse work;

(*b*) the advances by *G. morsitans* and (in the north-east) by *G. swynnertoni*, which are converging on Singida, and the effort that is being made to stop these advances.

Notes on points of special interest.

(i) On the right (east) of the map is shown the advance from Western Kondoa (*a*) to Singida, (*b*) into Usandawe, which country it has been overrunning rapidly. The progress of the advance is shown to the end of 1933. The barrier clearing (with settlement) is indicated by cross-hatching.

Long arrows pointing south-east below the word " Usandawe " show the route which the advance is expected to take into north-west Dodoma. It is probable that the advance could be stopped on the Bubu.

(ii) The Hika fly advance is travelling northwards from the railway. In 1933 it was wedged between two thickets. It is described on pp. 429–431 above.

(iii) In the extreme south of the area shown on the map will be seen the area of unsuitable wooding, represented by numerous T's (indicating dry thorn-bush), which has stopped an advance eastward by *G. morsitans*.

(iv) Kazikazi and the thickets in which Burtt's investigations took place lie on the railway in the western part of the area shown on the map. Greater detail is given in pl. 20, fig. 2. In the explanation on the map, read " duricrust " for " duriecrust."

(v) Further north and shown in the centre of the left-hand margin of the map, is a black line in the form of a small arc with a road passing through it from Matabele (illegible on the map) to Singida. This arc represents the point reached by the flies in 1929. The flies were advancing between the end of the great thicket and the open Wembere Steppe, and through the two small gaps shown on the map, from the great western miombo-and-*morsïtans* belt (*see* area coloured red in map 1 and pp. 431–433).

By the end of 1933 this advance had reached a point (indicated by the long black curving line) lying to the north and west. In 1936, it is washing the barrier shown in cross-hatching to the north and is reaching the settled " cultivation steppe." To the north of the barrier is shown the miombo area (indicated on the map by rounded tree-cyphers) in the Mkalama district which is still liable to be infested if the barrier is crossed.

(vi) The curved line at the top of the map represents the advance southward and south-westward of the " Barabaig " belt of *G. swynnertoni* discussed on pp. 436 and 437 above. In front of it, there is suitable " dry thorn-bush " wooding (indicated by " TTT ") into which it can advance.

(vii) In the centre of the map is shown Maclean's " hexagon." The thicket on the southern side, east of the Singida railway is not shown on the map.

(viii) The great rift valley is shown approaching Singida from the north-east (*see* top right-hand corner of the map) and then turning south, south-west, and south-east again.

Explanation of map 7.

Preliminary survey of the game fauna of the Tanganyika Territory.

(*Note.* This map should be read in conjunction with map 1.)

1. Animal communities.

M1. The miombo animal community, *i.e.*, the animals of the miombo and allied types of wooding.

$M1^1$. Comprises sable antelope, Lichtenstein hartebeest and, south of the Rungwe, Sharpe's steinbuck, as characteristic species; zebra, giraffe, eland, the last often abundant; impala, where alternation of open, short grass and thicket is inset in the general wooding; oribi, greater bustard and sometimes wildebeest and ostrich in open mbugas, reedbuck in these and by reedy streams and on open grassy hills—the southern reedbuck (*Redunca arundinum*) south of the railway in the west, elsewhere the bohor (*Redunca redunca*); common waterbuck by streams and rivers; dikdik, chiefly north of the railway, where thickets are interspersed in the wooding. Greater kudu and bushbuck seldom in any numbers, and also, red duiker and bush-pig, where thicket-areas are present, the last two species particularly in the eastern "mesophytic" area shown in the map; rhinoceros in much of this area (but with elephant and buffalo this is usually shown under H); klipspringer and hyrax (*Procavia* and *Heterohyrax*) on rocky masses and rocky heights; baboon especially here but also in the general wooding; duiker (usually sparse), wart-hog, lion, leopard, occasional cheetah, hyaena and other carnivora; giraffe generally, but absent south of the Rufiji and east of a line drawn from Iringa to the north end of Lake Nyasa; vervet monkey (*Cercopithecus aethiops*); horned guinea-fowls (*Numida*) in the savanna wooding with interspersal of open; crested guinea-fowls (*Guttera*) in the thickets.

$M1^2$. The same as $M1^1$, with roan antelope and topi added.

NY. The nyika and plains animal communities: the animals of the dry thorn-bush or nyika and (for purposes of this map) also of the open plains that are associated with it. These communities are made up as follows:—

NY^1. Ostrich, greater and lesser bustards, secretary bird, zebra, Coke's hartebeest, white-bearded wildebeest, Grant's and Thomson's gazelles, oribi—all especially of the open plains; rhinoceros—plain, savanna and thicket; in the drier semi-desert bushed nyika, in areas west of the Great Rift, fringe-eared oryx, gerenuk, lesser kudu (where there are good thicket bases) and vulturine guinea-fowl, the former in the plains also; common steinbuck, dikdik, greater kudu (the dikdik and sometimes the kudu numerous where some thicket is present)—and duiker (mostly rather sparse); giraffe and eland, often in numbers, as much at home here as in the miombo; impala (numerous), reedbuck (bohor and, *e.g.*, on grassy scarptops and foothills, Chanler's), also waterbuck, bushbuck, klipspringer and its associates, the various carnivora, the vervet monkey (*Cercopithecus aethiops* and horned and crested guinea-fowls, all as described under $M1^1$. Sandgrouse are specially associated with NY^1 and NY^2. Baboons are abundant in the numerous granite kopjes and also in the riverine thickets with good trees.

NY^2. The same as NY^1, with roan antelope and topi added and oryx and gerenuk omitted.

PL. Only a few sites out of many are indicated thus in the map: the plains animals only or mainly of the NY^1 list, *i.e.*, to the first semicolon.

SSG. A section of PL. Animals of the seasonally swampy grass-lands or the open, grassy, non-swampy edges of permanent swamp—together, the "vlei" community; ostrich, greater bustard and lesser, oribi, reedbuck (southern or bohor), topi, within its range. The animals of the surrounding woodlands also graze out in the open. Such places in the dry thorn-bush are used by the NY animals.

SW. Swamp and water-margin animal communities. A few sites only indicated, but represented by the communities shown in West Bukoba, on the Malagarasi,

further south, under P (puku) in Mahenge, and on Lake Rukwa, and by many unmentioned waters. A great assemblage of various ducks and geese, as well as moorhens, coots, grebes, herons, bitterns and egrets, cormorants, darters, storks, pelicans, and flamingoes; hippopotamus, situtunga antelope, puku, waterbuck (defassa or common), reedbuck (these three less aquatic than the first three), water-mongoose, otter, in places water-porcupine, certain shrews, crocodile (*Crocodilus niloticus* and *C. gabonensis* in L. Tanganyika, only *niloticus* elsewhere) and monitor lizards.

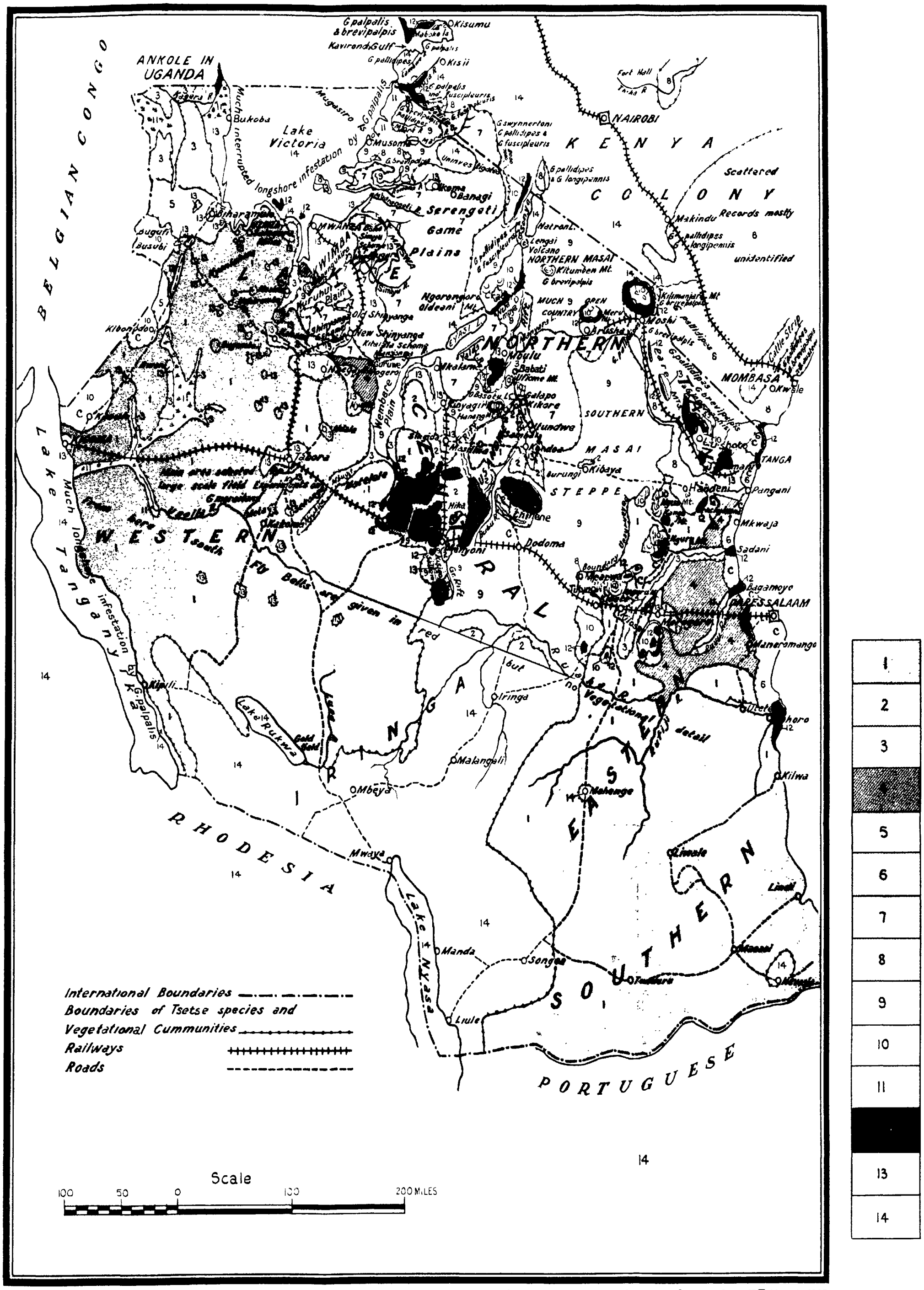
H. "Heavy" animals or those of "heavy" cover, the closed-cover communities. Elephant, rhinoceros, buffalo, both in heavy cover and out of it, to some extent (elephant) a matter partly of season, partly for interspersal of refuges; red forest duiker in rain forest and thickets, deciduous or conifer, from the coast, west to the latitude of Kilosa; bush-pig and leopard, the former in the eastern half of the country more especially and in the northern rain forests; crested guineafowls (*Guttera* spp.). Associated with all these, but living in the savanna wooding outside, giraffe (except in the south-east), eland, zebra, commonly impala, wart-hog, lion, leopard, hyaena, and the smaller carnivora.

C.Th. A subsection of H. Animals of the extensive thicket stretches of the coastal strip, inhabited by Suni and Harvey's duiker with, often, other animals out of H.

RF. Rain-forest animals—another sub-community of H (the closed-cover communities): tree hyrax, colobus and blue monkeys, red forest duiker, bushbuck (using mainly though deeply the margins), elephant, rhinoceros, buffalo, bush-pig, leopard, and a special assemblage of birds, including the crested guinea-fowl (*Guttera* spp.); in some forests, blue duiker. Rain-forest areas are not specifically shown in this map, but will be found in the vegetational map under "12" in various localities from the Ruaha river to the Kenya border. They should be distinguished there from the other climax communities—*i.e.*, the mangroves on the coast and the stigi deciduous-thicket system shown in the centre of the Territory.

2. Individual species.

AD	Abbott's duiker	Lch	Lichtenstein's hartebeest
All[d]	alleged	LK	lesser kudu
B	buffalo	O	ostrich
Bb	bushbuck	Ori.	oribi
Bd	blue duiker	O'x	fringe-eared oryx
Bp	bush-pig	P	puku
C	colobus monkey	R	roan antelope
CH	Coke's hartebeest	Rb	reedbuck (species unspecified)
Croc.	crocodile, in nearly all waters of any size	RB	bohor reedbuck
		RC	Chanler's mountain reedbuck
CW	common waterbuck	RD	red forest duiker
D	common duiker	RS	southern reedbuck
Dk	dikdik	S	sable antelope
DW	defassa waterbuck	Sit.	situtunga
E	eland	St	steinbuck
El	elephant	Su	suni or pigmy antelope
G	giraffe	T	topi
Ger.	gerenuk	TH	tree hyrax (*Dendrohyrax* spp.)
GK	greater kudu	Ty	Thomson's gazelle
Gr	Grant's gazelle	W	wildebeest
Hipp.	hippopotamus, in all waters of any size	W^1	Nyasa blue wildebeest
		W^2	white-bearded wildebeest
Im	impala	Wb	waterbuck (species unspecified)
K	kob	Z	zebra
Kl	klipspringer	*	very good tiger-fishing
L	lion		



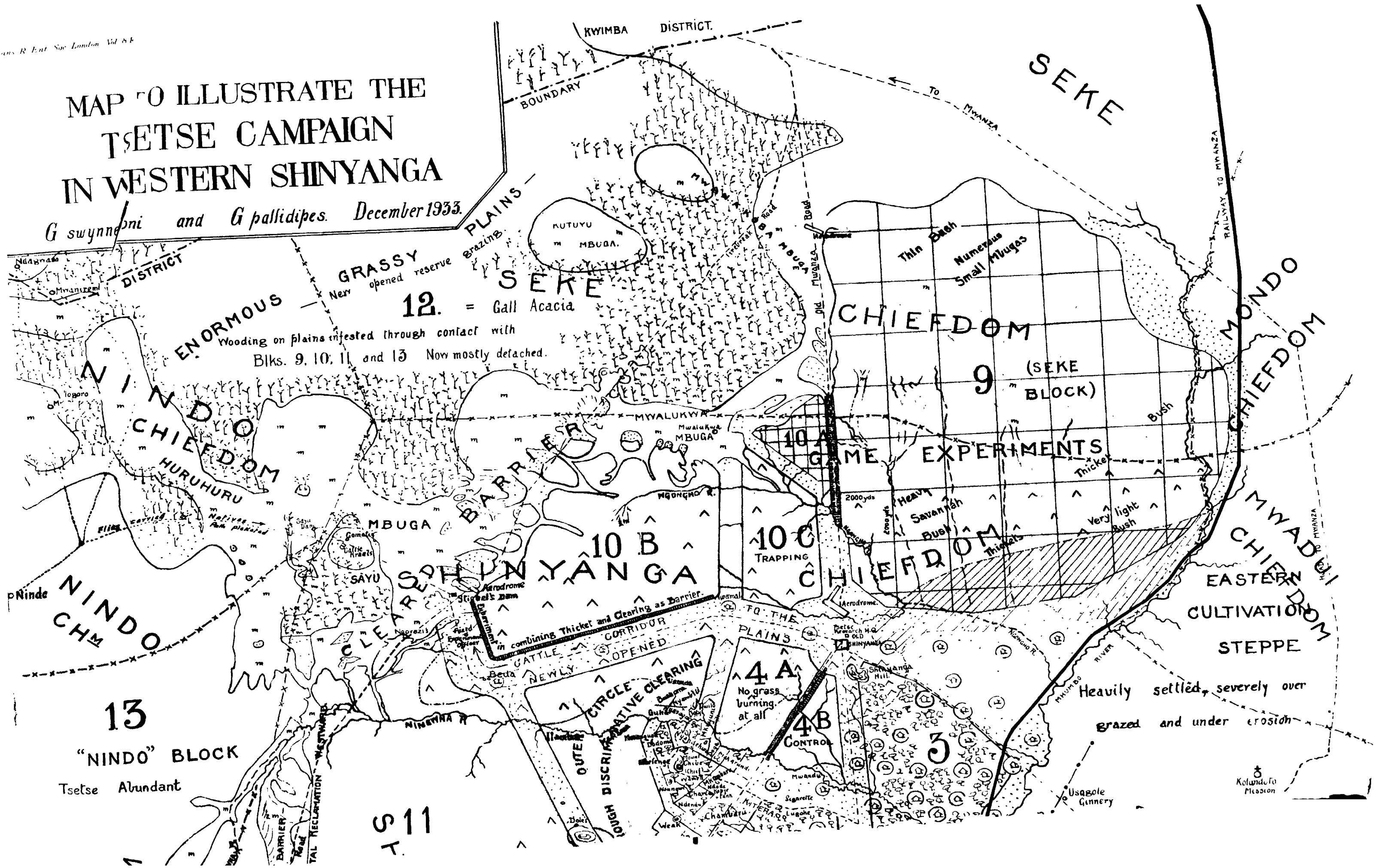
After Swynnerton. 1934. Drawn by Survey Dept. T.T. March, 1935.

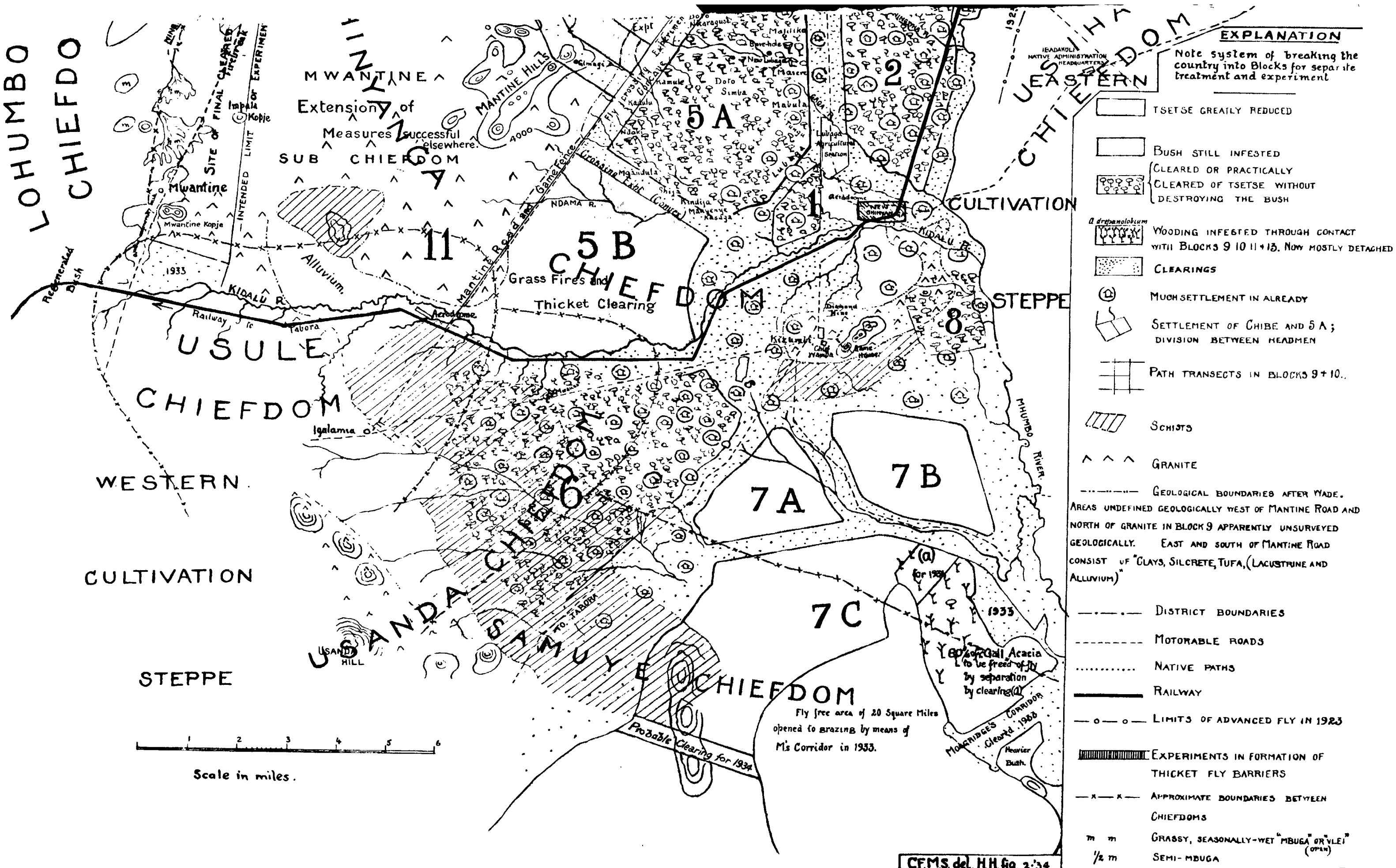
DISTRIBUTION OF TSETSE FLIES AND, PRELIMINARILY, THE VEGETATION IN TANGANYIKA AND SOUTH KENYA.

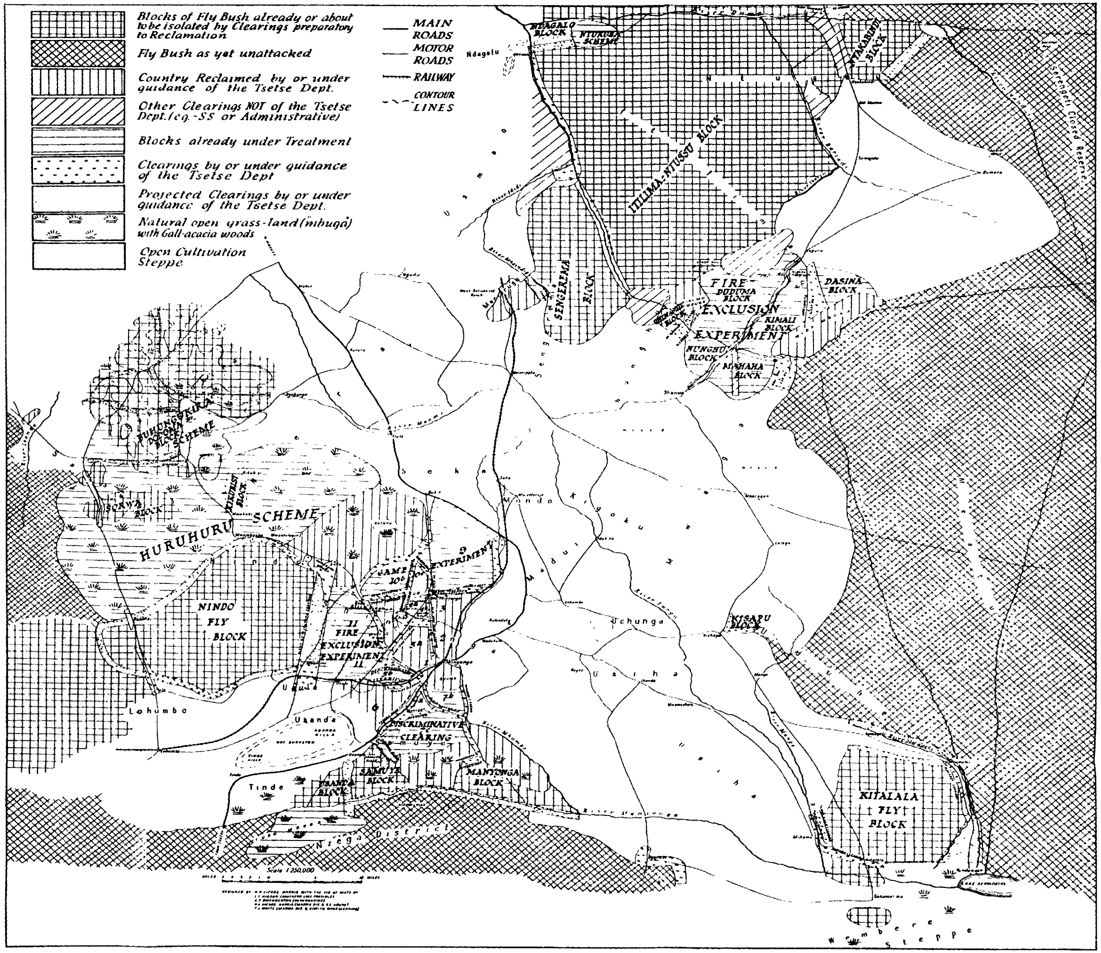
Trans. R. Ent. Soc. London Vol. 84

MAP TO ILLUSTRATE THE TSETSE CAMPAIGN IN WESTERN SHINYANGA

G. swynnertoni and G. pallidipes. December 1933.




EXPLANATION
Note system of breaking the country into Blocks for separate treatment and experiment
TSETSE GREATLY REDUCED
BUSH STILL INFESTED
CLEARED OR PRACTICALLY CLEARED OF TSETSE WITHOUT DESTROYING THE BUSH
WOODING INFESTED THROUGH CONTACT WITH BLOCKS 9 10 11 + 13. NOW MOSTLY DETACHED
CLEARINGS
MUCH SETTLEMENT IN ALREADY
SETTLEMENT OF CHIBE AND 5 A; DIVISION BETWEEN HEADMEN
PATH TRANSECTS IN BLOCKS 9 + 10.
SCHISTS
GRANITE
GEOLOGICAL BOUNDARIES AFTER WADE. AREAS UNDEFINED GEOLOGICALLY WEST OF MANTINE ROAD AND NORTH OF GRANITE IN BLOCK 9 APPARENTLY UNSURVEYED GEOLOGICALLY. EAST AND SOUTH OF MANTINE ROAD CONSIST OF "CLAYS, SILCRETE, TUFA, (LACUSTRINE AND ALLUVIUM)"
DISTRICT BOUNDARIES
MOTORABLE ROADS
NATIVE PATHS
RAILWAY
LIMITS OF ADVANCED FLY IN 1923
EXPERIMENTS IN FORMATION OF THICKET FLY BARRIERS
APPROXIMATE BOUNDARIES BETWEEN CHIEFDOMS
GRASSY, SEASONALLY-WET "MBUGA" OR "VLEI" (OPEN)
SEMI-MBUGA
LOHUMBO CHIEFDO
MWANTINE
Extension of Measures successful elsewhere.
SUB CHIEFDOM
NYANGA
MANTINE HILLS
4000
Mwantine
Mwantine Kopje
Impala Kopje
SITE OF FINAL CLEARED
INTENDED LIMIT OF EXPERIMEN
1933
Regenerated Bush
KIDALU R.
Railway to Tabora
Alluvium.
11
NDAMA R.
Mantine Road and Game Fence
5B
Grass Fires and Thicket Clearing
CHIEFDOM
Aerodrome
5A
Kamule
Doro
Simba
Mabula
Matilika
Kadulu
Ndaki
Mganduda
1
2
Lubaga Agricultural Station
HEADQUARTERS NATIVE ADMINISTRATION
EASTERN
CHIEFDOM
CULTIVATION
STEPPE
8
Diamond Mine
Kizumbi
Game House
USULE
CHIEFDOM
Igalamia
WESTERN
CULTIVATION
STEPPE
6
7A
7B
7C
MHUMBO River.
1933
Gall Acacia to be freed of fly by separation by clearing (a)
Heavier Bush.
MORRIDGE'S CORRIDOR Cleared 1933
USANDA SAMUYE CHIEFDOM
USANDA HILL
TO TABORA
Probable Clearing for 1934
Fly free area of 20 Square Miles opened to grazing by means of M's Corridor in 1933.
Scale in miles.
1
2
3
4
5
6
CEMS del. HH fig. 2.'34



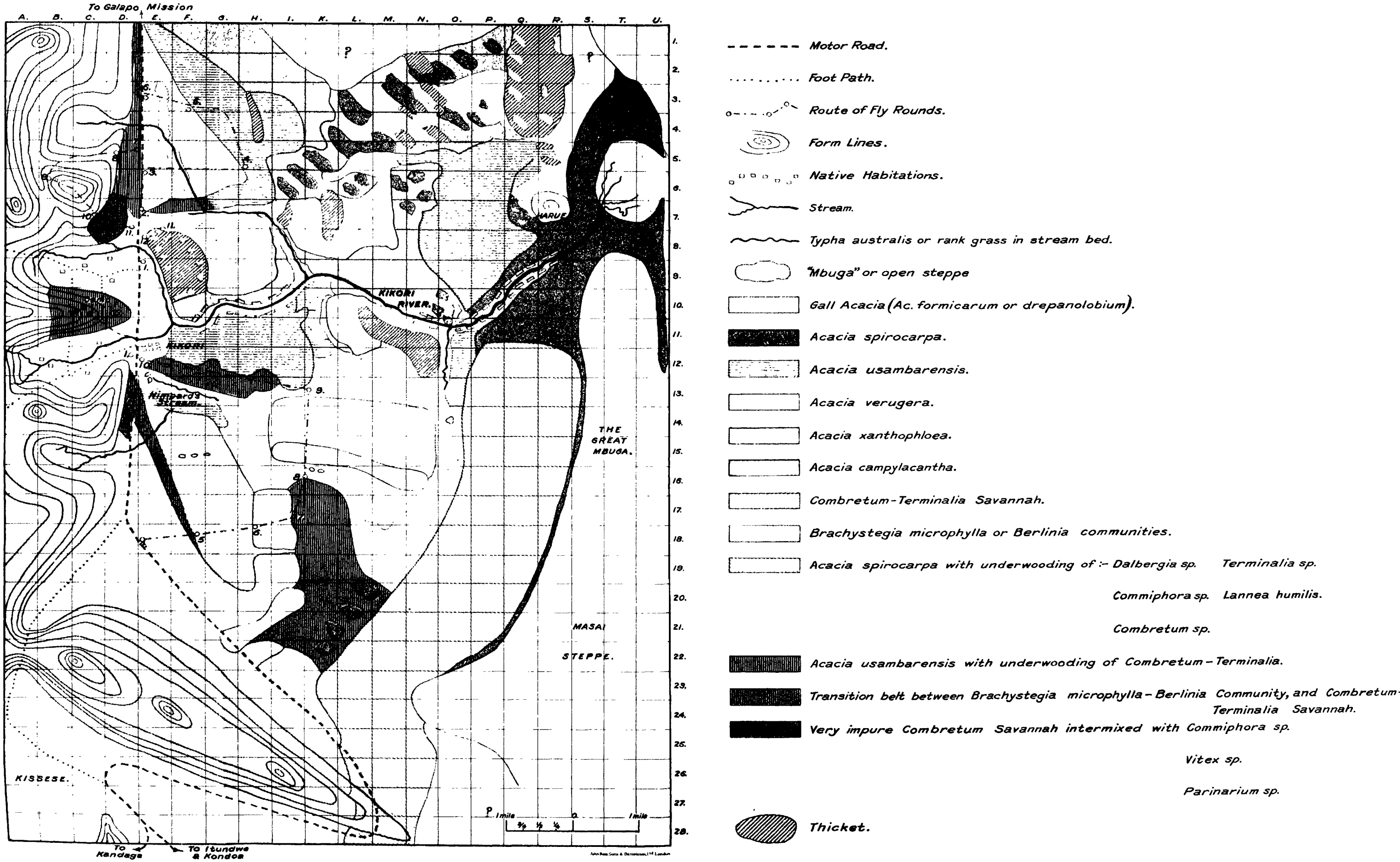
An impression of the tsetse campaign in the LAKE PROVINCE OF TANGANYIKA TERRITORY

Showing a Comprehensive Plan, already well advanced, of division into Blocks, great and small, and attack.

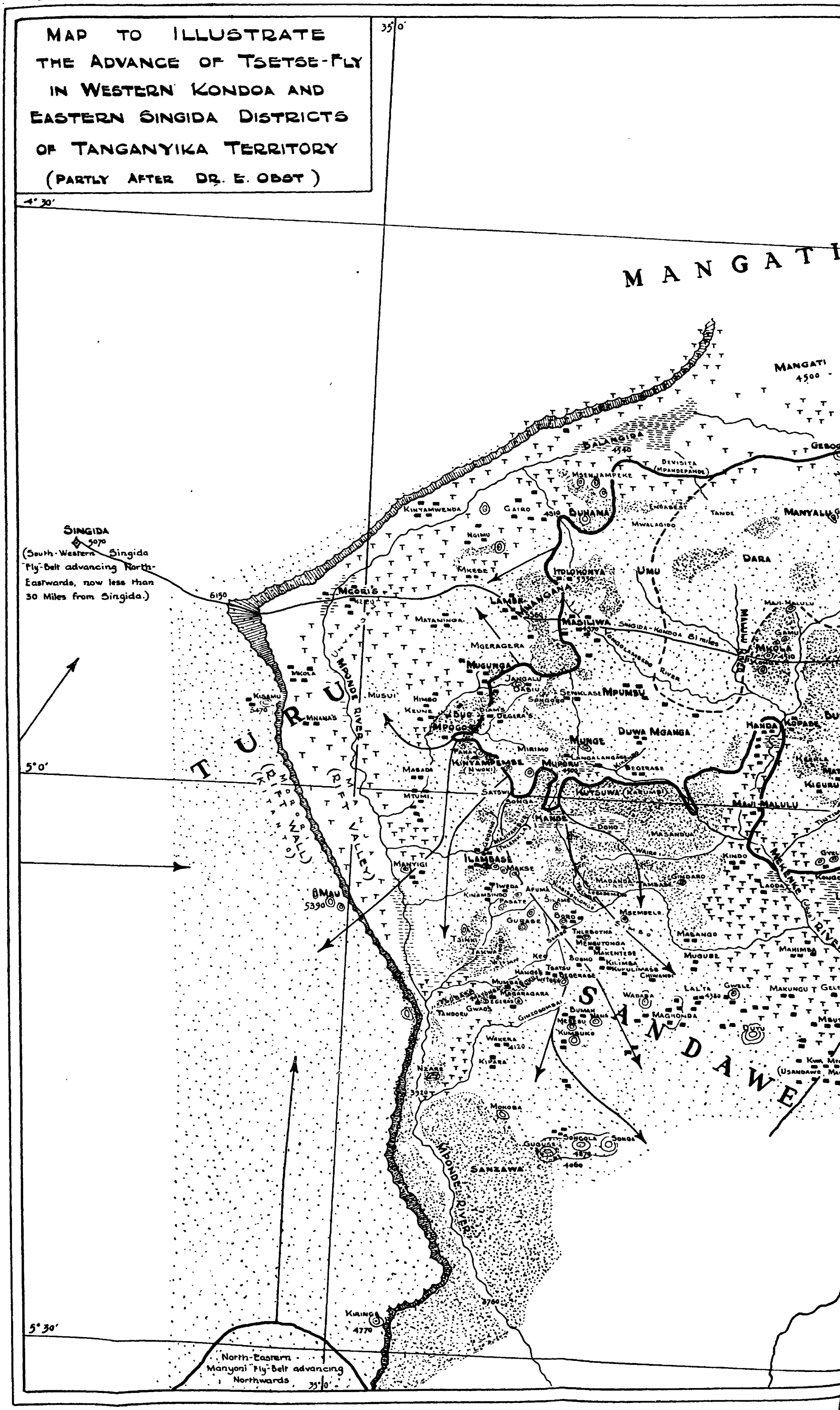
The tsetse campai

This map gives an imp of Tanganyika Territory. trates a comprehensive pl country has already been on the problem is in progr Reference should be dealing with reclamation .

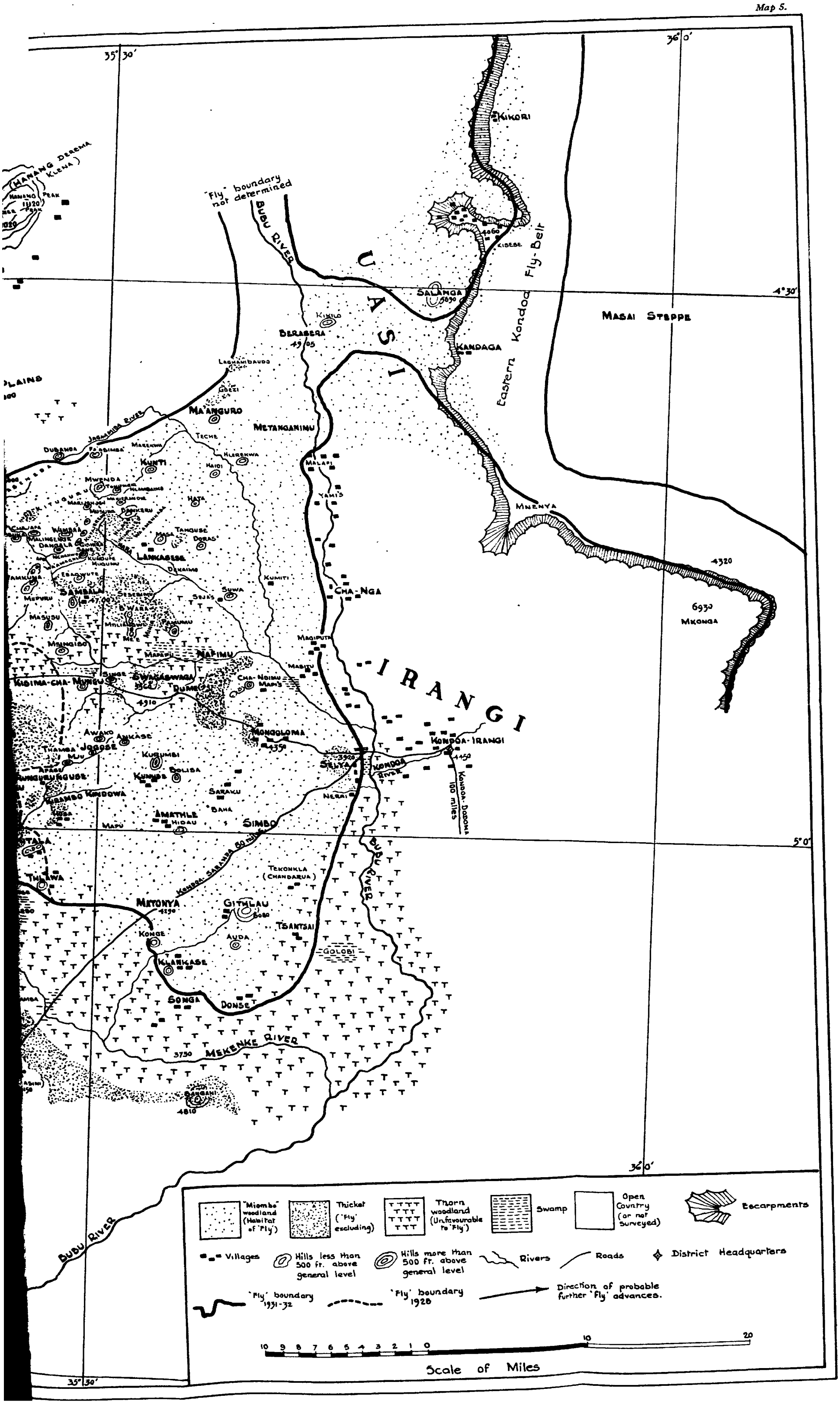
1. Through, and to th (left centre of the map). hatching above with the 2. The word " Maria should read " Mataluga



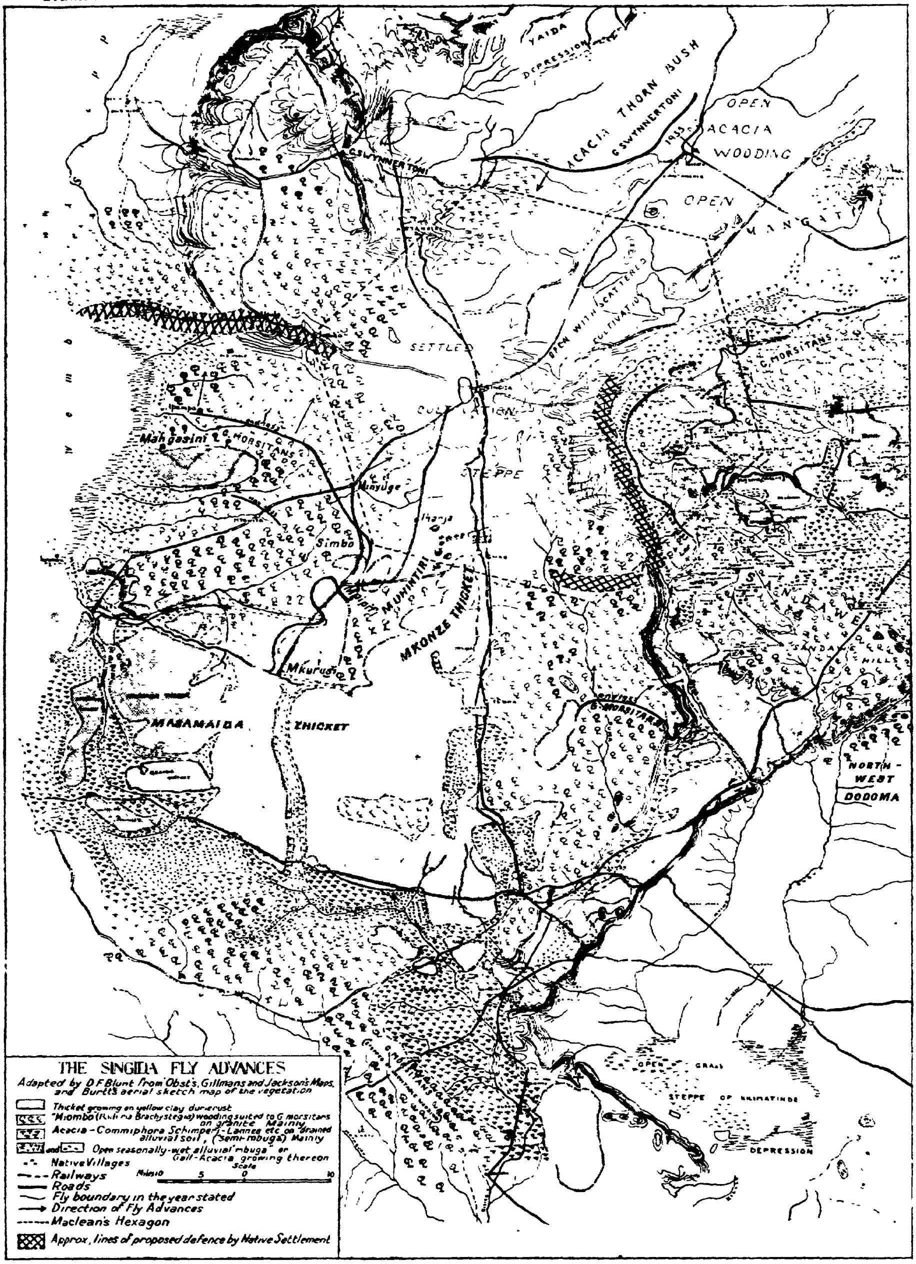
VEGETATIONAL MAP OF THE KIKORI DISTRICT.



MAP TO ILLUSTRATE THE ADVANCE OF TSETSE-FLY IN WESTERN KONDOA AND EASTERN SINGIDA DISTRICTS OF TANGANYIKA TERRITORY
(PARTLY AFTER DR. E. OBST)
35° 0'
4° 30'
5° 0'
5° 30'
MANGATI
MANGATI 4500
SINGIDA 5070
(South-Western Singida Fly-Belt advancing North-Eastwards, now less than 30 Miles from Singida.)
6150
TURU
SANDAWE
MPONDE RIVER
(RIFT VALLEY)
(RIFT WALL)
BALANGIDA 4540
MAU 5390
KIRINGA 4770
SANZAWA
MANYIGI
ILAMBASE
MGORI'S
MUGUNGA
KINYAMPEMBE
MPOGO
MPUMBU
MUNGE
DUWA MGANGA
HANDA
MAJI MALULU
MKOLA
DARA
UMU
MANYALU
BUHAMA
ITOLOMONYA 5334
MNANGANA
MASILIWA
Singida-Kondoa 81 miles
MKEKE RIVER
North-Eastern Manyoni Fly-Belt advancing Northwards



35° 30'
36° 0'
4° 30'
5° 0'
KIKORI
"Fly" boundary not determined
BUBU RIVER
U A S I
SALANGA
KANDAGA
Eastern Kondoa Fly-Belt
MASAI STEPPE
BERABERA
MA'ANGURO
METANGANINU
MNENYA
KUNTI
SAMBALI
CHA-NGA
6930
MKONGA
4320
NAPIMU
I R A N G I
KISIMA-CHA-MUNGU
SWANGWAGA
DUMB
MONGOLOMA
KONDOA-IRANGI
KONDOA RIVER
SELYA
Kondoa-Dodoma 100 miles
JOGOSE
AMATHLE
SIMBO
BUBU RIVER
THAWA
METONYA
GITHLAU
TSANTSAI
GOLOBI
KLANKASE
SONGA
DONSE
MEKENKE RIVER
BUBU RIVER
"Miombo" woodland (Habitat of 'Fly')
Thicket ('Fly' excluding)
Thorn woodland (Unfavourable to 'Fly')
Swamp
Open Country (or not surveyed)
Escarpments
Villages
Hills less than 500 ft. above general level
Hills more than 500 ft. above general level
Rivers
Roads
District Headquarters
'Fly' boundary 1931-32
'Fly' boundary 1928
Direction of probable further 'Fly' advances.
10 9 8 7 6 5 4 3 2 1 0 10 20
Scale of Miles



THE SINGIDA FLY ADVANCES
Adapted by D F Blunt from Obst's, Gillmans and Jackson's Maps, and Burtt's aerial sketch map of the vegetation
Thicket growing on yellow clay durierust
"Miombo (... Brachystegia) wooding suited to G morsitans on granite Mainly
Acacia - Commiphora Schimperi - Lannea etc on drained alluvial soil, ("Semi-mbuga") Mainly
Open seasonally-wet alluvial "mbuga" or Gall-Acacia growing thereon
Native Villages
Railways
Scale
Miles 10 5 0 10
Roads
Fly boundary in the year stated
Direction of Fly Advances
Macleans Hexagon
Approx, lines of proposed defence by Native Settlement
YAIDA DEPRESSION
ACACIA THORN BUSH
G SWYNNERTONI
OPEN
ACACIA
WOODING
OPEN
MANGATI
SETTLED CULTIVATION
STEPPE
G. MORSITANS
Mahgasini
Minyuge
Simbo
Mkurusi
MUHINTIRI
MKONZE THICKET
MASAMAIDA
THICKET
SANDAWE
NORTH - WEST DODOMA
OPEN GRASS
STEPPE OF KHIMATINDE
DEPRESSION

A PRELIMINARY SURVEY OF THE GAME FAUNA OF TANGANYIKA TERRITORY.